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CONTRIBUTIONS IN MATHEMATICS, PHYSICAL AND BIOLOGICAL SCIENCES

DOCTRINA VIM PROMOVET INSITAM

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Three numbers of the Journal are published every year, in April, August and December respectively and contributions for publication should be sent to the Editor not later than February 1, June 1, and October 1 respectively.

Contributors are requested to be clear and concise. Manuscripts should not exceed 8,000 words and should be in a final form for the press. Each paper should start with a short summary which should be an abstract of the whole paper, complete and clear in itself, and not over 3 per cent. of the length of the paper. The introduction and reviews of literature should be restricted to closely pertinent papers.

The manuscript should be typewritten on one side of the paper only, with wide margins and be double spaced throughout including titles, footnotes, literature citations and legends. Symbols, formulae and equations must be written clearly and with great care. Scientific names of genera and species are printed in italics and should be underlined in the typescript. Too many tables, graphs, etc. should be avoided. Each table should be typed on a separate sheet with its proper position marked in the text in pencil.

Literature citations: All references to literature cited in the text should be presented together at the end of the paper in alphabetical order of authors' names. Each reference should be given in a standard form as follows: (1) name(s), followed by initial(s), of author(s); (2) year of publication in brackets; (3) full title of paper; (4) title of journal, abbreviated according to *World List of Scientific Periodicals*, 1952, and underlined; (5) volume number in Arabic numerals, underlined with two lines to indicate bold type; (6) page numbers without the prefix, p. When books are mentioned in the references, the order should be: name of author(s), initial(s), year in brackets, title of the book, which should be underlined, volume number, edition, page, followed by place of publication and name of publisher. Where a reference has not been seen in original, it should be indicated by an asterisk and the name of the abstracting journal or other source should be mentioned in brackets. If the title is in a language other than English, the diacretic signs, etc., should be precisely given as in the original.

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Biology of Myllocerus subfasciatus Guerin*

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BY

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(Received for publication on February 2, 1958)

SUMMARY

The life history of the weevil *Myllocerus subfasciatus* G. a typical leaf eating form of weevil and a pest of brinjal, potato, apple and pear in South India is given in detail. The descriptions of various stages of the weevil and the various aspects of its biology are given in detail for the first time.

Introduction

Myllocerus subfasciatus Guerin is one of the injurious forms of leaf eating weevils of the genus *Myllocerus* occurring in South India. It is a serious pest of Brinjal (Solanum melongena) in the plains and Potato (S. tuberosum) in the hills. It occurs every year on brinjal grown in the College Farm at Coimbatore and causes considerable damage to the crop. Since the life history of the weevil is unknown detailed studies on the biology of the pest were made and the results are presented in this paper.

History and Systematic Position

Myllocerus subfasciatus G., belongs to the sub-family *Otiorhynchinae* of the family *Curculionidae*. The species was first described by Guerin (1843) from Nilgiris. Later Marshall (1916) gave more detailed description of the species. Fletcher (1919) and Ramakrishna Ayyar (1922, 1932, 1940) have mentioned the distribution and host plants of the weevil. Apart from these there is no information about this weevil and nothing is known of its life history and habits.

* Formed part of thesis submitted For M.Sc. of Madras University in 1954.

Distribution

The weevil is distributed in Burma, Ceylon, Bombay and Central Provinces (Fletcher 1919). It is distributed throughout South India.

Host plants, Nature and Symptoms of Damage: The weevil feeds on brinjal in plains and potato, apple and pear in the hills. It is also recorded on *Acacia decurrens* (Rau 1936). Both adults and grubs do damage to the crop, the adults cause defoliation and the grubs feed on roots. Adults cause more serious damage. They congregate in large numbers on tender foliage and nibble leaves starting their attack from the margins and working towards the midrib and finally consume the entire leaf blade. In severe infestation the plants show only the midrib and veins. The grubs feed on tender roots and when large number of them attack the root of the same plant, the general vigour of the plant is much affected with the result it becomes stunted in growth. In severe infestations the yield of the crop is much affected as much of the leafy matter is lost. At Coimbatore the weevil is found throughout the year on brinjal, as it is raised in both summer and rainy seasons and there will be a continuous crop. The active period of the adults is from beginning of August to end of January in the rainy season crop and from April to July in summer crop. The pest has been noted to cause more damage to summer crop than that raised in rainy season.

Life History, Bionomics and Descriptions of Various Stages

Copulation and Oviposition: The weevils copulate soon after emergence and the duration of the copulation varies from 15 to 20 minutes. They copulate freely both in the field and laboratory. The weevil lays eggs in soil to a depth of 5 to 10 mm. In captivity they lay eggs in instalments and the interval between the two successive instalments vary. Eggs are laid in small clusters of about 10 to 30 each. The number of eggs laid by a single female was found to vary from 117 to 499 with an average of 333·9. The pre-oviposition and oviposition periods varied from 7 to 23 days and 31 to 89 days with an average of 14·3 and 65·8 days respectively.

Egg: Egg is oval, smooth and white, the colour changing to deep brown just before hatching. It measures on an average 0·53 mm in length and 0·33 mm in width. The egg period was

found to vary from 6 to 7 days with an average of 6·4 days when the average maximum and minimum temperatures and humidity in the laboratory were 87·7°F, 78·6°F, and 81·1% respectively.

Grub : The grub passes its entire life inside the soil and hence it was found difficult to determine the number and duration of instars. However they could be divided into ten groups by measuring head widths and application of Dyar's law. The average measurement of head width in each group tallied closely with the expected width calculated by Dyar's law. The details are furnished in the table on the next page.

The characters of the grubs in each of these instars are similar and difference is found only in the measurements as detailed above. The description of first and full grown grubs are given below. The description of the grub is made for the first time.

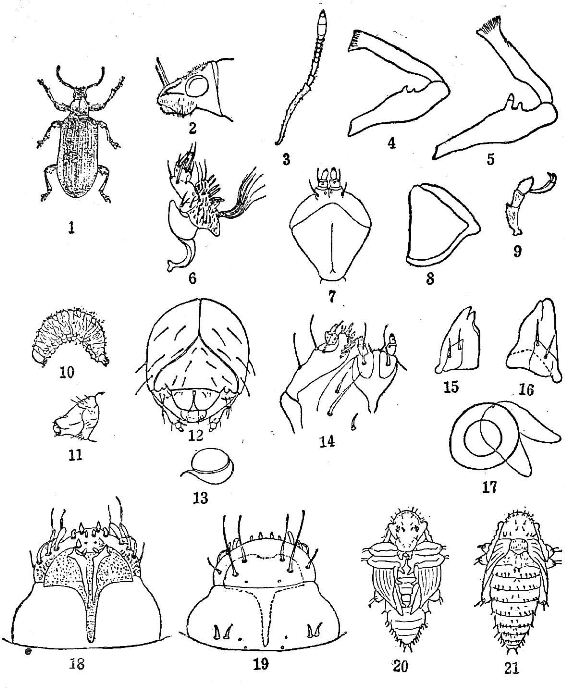
First instar grub : Apodous. Colour pale white. Body cylindrical, posterior end tapering and truncated distally. Head light brown, smooth and as long as broad; frons without any median dark line; mandibles prominent and bifid. The whole body is finely setose.

Full grown grub : Apodous. Colour pale white. Body cylindrical, fleshy, moderately curved and tapering more strongly posteriorly. Head capsule chitinised, pale brown. Epicranial suture distinct, half as long as epicranium. Frontal sutures distinct, each arm about one and half times longer than epicranial suture; each half of epicranium bears six setae. Frons wider than long without dark median line and bears four pairs of setae. Antenna with apical segment a transverse oval cushion borne on a slightly wider basal skin. Clypeus three times broader than long and bears four short setae at the base. Labrum twice as broad as long, anterior margin rounded and posterior margin with a median parellel sided brown extension which extends back to epistoma under clypeus; the dorsal surface with two pairs of long and one pair of short setae. Epipharynx with two very strongly chitinised rods which are wider apart distaly and extend to about anterior margin of the clypeal zone; the anterior margin with three long anterolateral setae on each side and a median row of four setae and two short post apical setae; between the rods are two pairs of short stout setae; the anterior pair placed more widely between the apices of the rods; in addition two tripartite pores are found between the rods; the whole epipharynx with numerous skin points

Instar	No. of grubs examined	HEAD Width in Millimetres Observed Min.	Max.	Mean	Calculated	Mean length in mm.	BODY Mean length in mm.	BODY Mean width in mm.
1 ..	100	0·22	0·23	0·21	0·21	0·21	0·48	0·24
2 ..	39	0·24	0·26	0·25	0·25	0·26	0·81	0·25
3 ..	42	0·30	0·33	0·31	0·30	0·34	0·92	0·36
4 ..	29	0·38	0·41	0·39	0·39	0·42	1·22	0·41
5 ..	32	0·45	0·47	0·46	0·44	0·51	1·61	0·65
6 ..	50	0·50	0·54	0·53	0·53	0·62	2·50	0·94
7 ..	49	0·66	0·62	0·64	0·64	0·71	3·40	1·20
8 ...	38	0·76	0·80	0·78	0·77	0·82	4·20	1·52
9 ..	53	0·93	0·96	0·95	0·93	1·10	5·40	2·10
10 ..	72	1·11	1·21	1·18	1·13	1·50	6·40	2·70

posteriorly. Mandibles flattened longer than wide, narrow towards apex which is bifid in case of freshly moulted larva and blunt just before moulting; outer face with a pale thin skinned patch near base and with two setae. Maxilla elongated with unsegmented mala, consisting of ten to twelve stiff rods, palpus two segmented, the basal segment longer than broad with a minute seta and a pair of sensory pores; apical one distinctly longer than broad with a single sensory pore and some minute sensory pegs at the tip; stipe with three long setae. Labium with two jointed palpi; apical segment longer than broad with one sensory pore and sensory pegs at the tip; basal joint longer than broad with one sensory pore; posteriorly the labium is limited by a Y shaped chitinised band and with one pair of long setae on each labial stipe; ligula with two pairs of setae anteriorly; subfacial region entire with three setae on each side. Prothorax transverse; pronotal plate pale testaceous, the terga simple with 6 to 8 pairs of setae. Meso and metathorax divisible into prescutum and scutoscutellum each with a row of setae. Abdomen ten segmented; segments 1 to 8 with three distinct transverse folds viz. prescutum; scutum and scutellum all provided with numerous setae. The nineth segment cylindrical, tapering towards basally with hardened skin and truncate distally; the truncate face with two parts, an upper and lower between which the anal segment projects; the upper part with crenulate dorsal margin and six bristles, the lower smaller with four bristles; abdominal sterna each with a transverse row of six to eight conspicuous acute brown bristles each giving one or two brushes. Spiracles small circular without air tubes.

Duration of larval stage : As the grubs pass their entire life inside the soil the following method was adopted for determining the larval period. A number of potted plants of brinjal were taken and the soil near the roots was raked up to a depth of one or two inches and a definite number of grubs hatched out from eggs obtained in the laboratory was introduced in each and covered with the soil. The pots were examined at frequent intervals to study the progress of the larval growth, In the course of these observations the date when pupae were found was recorded and this gave the approximate larval period of the insect. Since this gave some indication of the approximate larval period, further rearings were done in a similar way but this time full grown grubs were removed and could be reared in the laboratory until they pupated which gave actual larval period. For detemining the



TEXT FIGS. 1-21. *Myllocerus subfasciatus.* 1. Adult. 2. Side view of head. 3. Antenna. 4. Front femur and tibia. 5. Hind femur and tibia. 6. Maxilla (Adult). 7. Labium (Adult). 8. Mandible (Adult). 9. Tarsus. 10. Grub. 11. Posterior extremity of the grub. 12. Head capsule of the grub. 13. Antenna of grub. 14. Maxilla and Labium of grub. 15. Mandible of freshly moulted grub. 16. Mandible of a grub before moulting. 17. Spiracle. 18. Epipharynx of grub. 19. Labrum of grub. 20. Pupa ventral view. 21. Pupa dorsal view.

actual larval period 20 potted plants were used and a total of 1180 grubs were introduced at different dates out of which only 229 full grown grubs were obtained and among these only 189 reached the pupal stage in the laboratory. The larval period for this number ranged from 62 to 75 days with an average of 65·1 days.

Prepupa : The length at this stage is about 6 mm. This stage lasts for only one day.

Pupa : Average length 6·0 mm; width 2·0 mm. General colour creamy white but turns darker before transformation into adult. Body with prominent tubercles with setae. Head a little narrower than prothorax and provided with three pairs of seta originating from prominent tubercles as follows: one pair in the middle, one pair at the upper edge of eyes laterally and one pair near the inner margin of the eye case. Rostrum a little longer than broad and provided with three pairs of setae raised on small tubercles. Prothorax wider than long with nine pairs of setae on prominent tubercles consisting of four anterior, two median and three posterior pairs. Mesothorax with six pairs of setae and metathorax with five pairs of setae. Legs folded and covered by wings; each femora with a pair of setae at distal end. Abdomen nine segmented; segments 1 to 8 have dorsally a transverse row of four pairs of setae on prominent tubercles on the posterior margin consisting of one median and three lateral pairs; in addition one pair present on the pleural region; anterior margin of each segment bears a pair of dorsomedian setae. The nineth segment bears a pair of short stout incurved spines at the apex, each borne in a somewhat prominent tubercles.

The grubs pupate in the soil in an ovoid earthern cell prepared by them (Pl. III, Fig. 6). Normally the pupal cells are found from 4 to 12 inches below the surface of the soil. The duration of pupal stage varied from 10 to 12 days with an average of 10·4 days for 112 individuals.

Total life cycle : It may be stated here that out of 229 grubs obtained from the pots in which 1180 just hatched grubs were introduced only 189 pupated in the laboratory and out of this number only 112 reached the adult stage. The total life cycle for these 112 individuals varied from 79 to 92 days with an average of 83·9 days, the average egg, larval and pupal periods being 6·7, 66·5 and 10·4 days respectively.

Adult: The detailed description of the weevil has been made by Guerin (1843) and Marshall (1916). The adult is an active greyish brown beetle found gregariously feeding on leaves during day and night. When disturbed the weevil feigns death. It is rarely seen in flight, though provided with well developed wings. It is positively phototropic. The duration of adult life observed on 25 individuals in each sex with and without food was found to vary from 51 to 110 days with an average of 72·3 days with food and 4 to 13 days with an average of 8·3 days without food for females and for males from 38 to 108 days with an average of 71·9 days and 3 to 11 days with an average of 7·7 days with and without food respectively.

Acknowledgements: The author is thankful to Sri K. P. Ananthanarayanan retired Entomologist, Coimbatore for his guidance and suggestions in this study. He is grateful to Mr. Eric Gowing Scopes, Kent for furnishing original descriptions and other references pertaining to the species, and to Mr. Van Emden, British Museum, London for advice given in the study of larval morphology.

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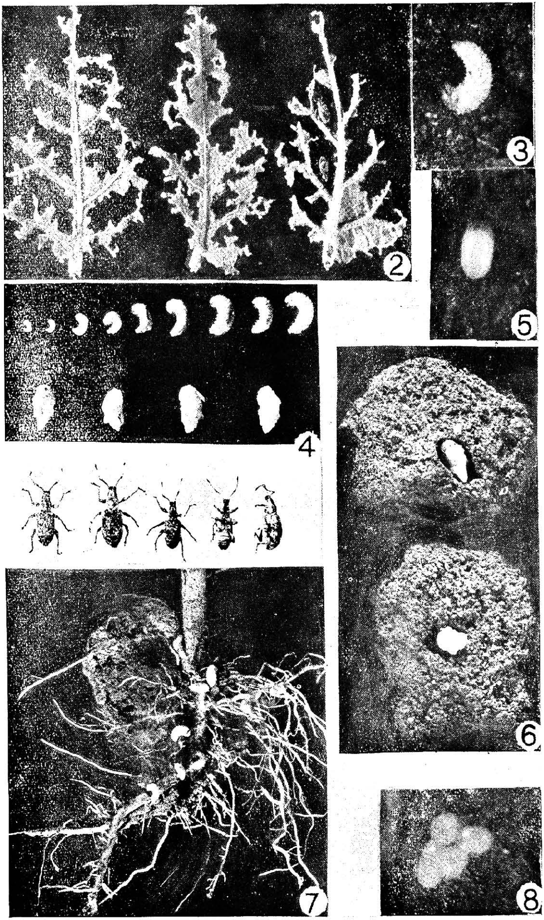
EXPLANATION OF PLATES II AND III

Plate II, Fig. 1. Brinjal plants showing Weevil damage.

Plate III, Figs. 2-8. Fig. 2. Brinjal leaves damaged by Weevils and Fig. 7. Brinjal roots showing grubs of the weevil; Figs. 3-6, 8 *Myllocerus subfasciatus*: Fig. 3. First instar grub (highly magnified); Fig. 4. grub and adults; Fig. 5. Egg; Fig. 6. Earthen pupal cell containing the pupa; Fig. 8. Cluster of eggs.

T. R. SUBRAMANIAN



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New Bearings in Embryology

BY

R. V. Seshaiya

I am thankful to the Syndicate of the Madras University for inviting me to deliver the Sir S. Subramanya Iyer Endowment Lectures. Sir S. Subramanya Iyer was a great jurist, scholar and patriot, and I consider it an honour to deliver these lectures associated with his name.

I have chosen as the subject of my lecture *"New Bearings in Embryology"*, in view of the fascination, the several unsolved riddles and the prospective importance presented by this rapidly developing branch of biology.

To observe at first hand the orderly progress of the development of any organism is an unforgettable experience, and to one who has watched, as I have had the opportunities to do, the orderly succession of kalaeidoscopic changes during the embryonic development of varied animals types of different *phyla,* no other aspect of biology appears so fascinating as embryology.

Apart from its fascination, the phenomenon of development is certainly the most puzzling of the unsolved problems of biology. How from a speck of protoplasm there develops an animate creature with characteristic pattern and organised structure, with potentialities for varied but well co-ordinated and 'purposive' behaviour, is certainly the most intricate of biological problems. According to Bonner[1], T. H. Morgan is supposed to have said in a lighter moment that he had switched over his investigations from embryology to genetics, as the latter was easier of analysis than the problem of regeneration — an aspect of development which he had tried to solve. The phenomenon of development continues to present the same difficulties to-day as at the time when Morgan divorced his first love and successfully wooed genetics.

All problems in biology, whether fundamental or applied in the last analysis, bear on a central theme, the spatial as well as

1. Bonner, J. T. 1952. *Morphogenesis,* An essay on Development, p. 3.

temporal diversity of organisms. The diversity of species which has come about in the long range of time-scale of organic life on the earth, i.e., during millions of years, constitutes the problem of evolution. Diversity viewed over a shorter range of the time-scale among parents and offspring is the subject of genetics. Diversity over a still shorter range, and its 'becoming' in ontogeny at different levels, constitutes the problem of embryology. Genetics, as defined by Bateson, is Physiology of Descent, and we may define embryology as Physiology of Ontogeny.

Modern biology is about a hundred years old. The second half of the nineteenth century witnessed the birth and triumph of the theory of organic evolution. The first fifty years of the present century witnessed the resurrection of Mendel's work and the phenomenal triumph of Genetics under the leadership of T. H. Morgan. The inequalities of living organisms, which may be due either to the recombinations of the old, or the emergence of the new, have been traced, as is well known to students of biology, to the genes, which are physical entities with precise location in the chromosomes, and with each so precisely coordinated with all the rest in the gene-complex as to result in the expression of definite characters in the organism.

The biologist now asks '*Quo Vadis*' ? What promises to be the main line of advance in biology during the next fifty years? The emphasis cannot hereafter be so much on how new charcters or recombinations of old arise, as on how the complex genotype which is responsible for the characterization of the organism can also bring about the progressive increase in organization during development so as to result in the phenotype. The emphasis in genetics is on the probabilities of genic recombinations and mutations which produce the differences between parents and offspring, but in embryology the emphasis shifts to the *certainty* of the development of an individual with characteristic organization and general pattern like that of the parent, and the determination of this organization during development. It is not characterisation, then, but the progressive increase of organization that is the focus of the embryologists' attention. To take an example employed by Woodger,[2] geneticists do not as a rule trouble about noses, but about the probabilities of noses being long or short, blue or red, and so on. The embryologist, on the other hand, is concerned

2. Woodger, J. H. 1929. *Biological Principles,* London.

with the development of an organism having as an integral part a nose which appears at the proper time and in the proper place. How are the characters of the organism, immanent and unrealised in the intricate complex of thousands of genes in the egg, progressively realised at increasing levels of organization to produce the phenotype? This is the chief problem now and hereafter in biology. Embryology, therefore, promises to occupy a pre-eminent place in biological investigations in the second half of this century. To quote from Sinnott's[3] recent and stimulating book, '*The Biology of the Spirit*', "here in the facts of growth and development are destined to be waged the most decisive battles of biology in future."

The problem of embryology as posed above might appear as a genetical problem to those who may have heavier leanings to the genetical approach in the study of living organisms. Goldschmidt[4] has referred to a discussion between Spemann and Valentin Haecker. Valentin Haecker had read at a meeting a paper in which he proposed the term "phenogenetics" for what some would call now 'physiological genetics'. In the discussion that followed Hans Spemann attacked him violently for trying to make others believe that he was doing something new by coining a new term while in fact he was just studying only one small fraction of embryology. Goldschmidt remarks that certainly both were right, and on the level of fundamentals embryology and phenogenetics are one and the same thing but different in their immediate aims. It all depends, as pointed out already, whether the bearings of the problem are for the moment characterisation or organization.

The significance of the present-day investigations in embryology and the possibilities of the future are best understood against the background of the past achievements.

Science, which is an aspect of human activity, owes its beginnings, in some instances at least, to the sense of wonder and spirit of enquiry inherent in man. Oftentimes the demands of life for food, shelter and clothing have been the sources of human scientific activity. But the progress of science is never uniform in time

3. Sinnott, E. W. 1956. *Biology of the spirit*, p. 14, London.

4. Goldschmidt, R. B. 1951. *In Genetics in the 20th century* (ed. Dunn, L.C.), p. 12.

or space. Influenced by historical events, social movements, intellectual outlook and cultural attainments, scientific investigations through centuries change their bearings and hypotheses. As observations progress and new data accumulate, experiments are devised to challenge the existing hypotheses, which may be discarded or modified or sublimated and new ones may be developed. Science often grows by moulting worn-out hypotheses and forming new ones.

Embryological enquiry, having no direct bearing on man's economic needs, grew out of man's curiosity about his pre-natal existence. Like many other branches of modern science, it has been usually traced to Hellenic origins. It was Aristotle in the 4th century B.C. who first posed the embryological problem correctly. His observations on the development of drones from eggs without fertilisation, on the yolk sac of the squid, viviparity of some sharks, gross changes in the chick development and his anticipation of the epigenetic concept of development are indeed remarkable achievements.

The pre-Aristotelean era in embryology was essentially a period of pure speculation without the foundation of factual observations. However, Needham[5] has remarked on the evidence of certain passages in the *Bhagavat Gita* that ancient Indian embryology reached a high level. A more interesting and accurate reference to human development is found in the *Garbha Upanishad*, which I understand, is an earlier work than the *Bhagavat Gita*. The *Garbha Upanishad's*[6] account of the changes in human development is as follows: *On the first night it is semi-fluid. In seven night it is like a bubble.* This is a correct reference to the blastocyst of modern embryology. *At the end of the month it is*

5. Needham, J. 1931. *Chemical Embryology,* Vol. I, p. 44, Cambridge.

6 **मास क्रमेण गर्भव्यक्ति भेदः**

एकरात्रोषितं कललं भवति। सप्तरात्रोषितं बुद् बुदं भवति। अर्धमासाभ्यन्तरेण पिण्डो भवति।

मासाभ्यन्तरेण कठिनो भवति। मासद्वयेन शिरः कुरुते। मासत्रयेण पाद प्रदेशो भवति।

अथ चतुर्थे मासे जठर कटि गुल्फ प्रदेशो भवति।

पञ्चमे मासे पृष्ट वंशो भवति। षष्टे मासे नासाक्षि श्रोत्राणि भवन्ति। सप्तमे मासे जीव संयुक्तो भवति। अष्टमे मासे सर्व संपूर्णो भवति नवमे पीवति॥

(From *Garbha Upanishad*)

hardened. In the second month embryo the head of the *embryo* is half of the total length and the *Garbha Upanishad* describes this by saying *"in two months the head becomes"*. In the third month according to modern observations the feet become well differentiated and are no longer paddle-like as in the previous stages. The Upanishad says *"in three months the region about the feet becomes"*. During the fourth month the external genital organs develop from an indifferent neutral stage to those characteristic of either sex, and the belly increases in size in proportion to the head and the arms and legs are rotated into their final positions in which the elbows point backwards and the knee forwards, and the soles of the feet face downward. The description in the *Upanishad* is: *"in the fourth month the region about the stomach, and loins and also ankle becomes"*. In the fifth month the body axis is straightened and the Upanishad says *"the spinal column becomes"*. In the sixth month, the eyelids fused since the formation in the third month open, and the foetus, if born will breath, cry and squirm. *"In the sixth, the face and the region of the nose, eyes and ears become"* — is the description in the ancient text. The seventh month embryo is able to survive premature birth; the nervous system is sufficiently developed to meet the demands of independent life; the cerebral hemispheres develop to such an extent that they cover the whole of the rest of the brain and also show fissures and grooves. The foetus is also sensitive to touch, possesses the sensation of taste and can probably perceive the differences between darkness and light. The *Garbha Upanishad* says: *"in the seventh month it becomes united with Jiva"*. The eighth and ninth months are concerned mainly in giving the finishing touches to the foetus preparatory to being ushered into a new world, and the passage in the Upanishad says *"in the eighth month it becomes full* (of organs) *and in the ninth it fattens"*.

After Aristotle embryological enquiry passed into a long diapause. The middle ages, often referred to as the Dark ages in Europe, placed implicit reliance on ancient writings and revelled in enchained thought and made no contributions. However, Roger Bacon who lived in thirteenth century (and who was burnt at the stake for using his mind to think and enquire) has said: "There are four impediments to knowledge; first, too great dependence on authority; second, allowing too great weight to custom; third, the fear of offending the vulgar; fourth, the affectation of concealing ignorance by the display of a specious appearance of

knowledge". Let us trust that our age is free from these impediments to knowledge.

Apart from these impediments, the progress of embryology was handicapped by the rarity of opportunities and the lack of optical aids for observations. It was awakened nearly two thousands years after Aristotle by the contributions of Malpighi, Harvey and Wolff. Later, improvements of the microscope in the nineteenth century opened up new possibilities in biology. In the early part of the nineteenth century Schleiden (1804-81) and Schwann (1810-82) announced the cell theory, and this provided embryological investigations with appropriate bearings. Eggs and sperms came to be recognised as cells. Embryological progress reached a new landmark with the work of Karl Ernst von Baer, who laid the foundations of scientific embryology by introducing the comparative method in embryolological studies. Before von Baer, embryological observations were casual, — the only objective being accumlation of factual knowledge —, and these were clothed, with few notable exceptions, in uncoordinated descriptions reflecting preconceived ideas. The comparative method gave an insight into observations, speeded up the progress of embryology and has continued to be a valuable tool in embryological studies. von Baer discovered the mammalian ovum, observed the resemblances in embryonic development of different animal types and his concept of the germ layers as transitory units of embryonic organization provided a new objective for embryological investigations and a means of determining homologies of organs. The comparative method and the concept of germ layers, which we owe to von Baer bore rich fruit. Incidentally, it may be remarked that von Baer's work illustrates that progress in science depends not on accumulation of factual observations and descriptions but on the insight into them, in interpretation and integration of facts into a principle or hypothesis.

Comparative embryology inaugurated by von Baer had its fulfilment in the colossal work of Francis M. Balfour[7] (1851-1882), who during his short life of thirty-two years brought together all available information about the development of animals of various groups and presented to the world his two volumes of comparative embryology — a book which has been pronounced to be of almost priceless value.

7. Balfour, F. M. 1880. *Comparative Embryology.*

Meanwhile, the theory of organic evolution which Charles Darwin had propounded in 1858 — when Balfour was seven years old — received general acceptance in the biological world, and provided a very influential factor in the progress and orientation of embryological research. The embryonic resemblances between different vertebrate animal types, which von Baer had observed, came to be interpreted as resemblances between adult ancestral organisms and embryonic stages of descendants and as recapitulation in ontogeny of the ancestral adult characters. Charles Darwin made effective use of the evidence of recapitulation in presenting his case for organic evolution. Later, Haeckel, the high priest of *Darwinism* on the continent of Europe, promulgated his famous Biogenetic Law, or Recapitulationary doctrine which ordained the recapitulationary phenomenon as a causal factor in development. Leading embryologists from Balfour to MacBride devoutly subscribed to this new doctrine. Hypotheses are essential as scaffoldings for scientific work, for stimulating and guiding investigations, but when irrationally and injudiciously applied, prove to be, as Goethe said, cradle songs with which a master lulls his disciples to sleep. In fact, embryologists lulled by the recapitulationary hypothesis slept over the necessity for the experimentation and causal analysis of development, and embrylology instead of being a distinct line of biological enquiry degenerated to be the handmaiden of the theory of organic evolution. To add to the stock of examples of recapitulation for confirming the evolution theory, to plant a new genealogical tree, or at least graft a new twig on existing genealogical trees became the avowed objective of every embryological investigation. Discussing the asymetry in Gastropods, MacBride[8] wrote, "The most plausible explanation of the inequality of growth, in both torsion and twisting, is that in the ancestral gastropod the visceral hump fell over to one side as the animal took to crawling over uneven ground". So the sins of the ancestral gastropod are now visited upon its present-day progeny !

Thus from the view-point of causal analysis and experimentation the recapitulation theory clogged the wheels of embryological progress but it was of immense value in encouraging investigations in the development of varied types of organisms. The works

8. MacBride, E.W. 1914. *Text Book of Embryology,* Vol. 1, Invertebrata, p. 317, London.

of Balfour, Korschelt and Heider, and MacBride bear testimony to this, besides the innumerable original papers published in various journals. But it is surprising that even brilliant embryologists like Balfour and Hertwig held the view that in the investigation of development, a sufficient causal explanation of a stage had been given when the immediately preceding stage had been described.

But other biologists like Wilhelm His realised that further growth of the embryological science would be possible only by shedding the evolutionary hypothesis as a causal factor in development. Between 1878 and 1887, this moulting occurred, and embryology entered on a new phase as Modern Embryology. In the United States a brilliant team of embryologists including Wilson, Conklin, F. R. Lillie and others under the leadership of Whitman initiated cell-lineage studies with remarkable patience and skilful technique. This school succeeded in tracing back the different tissues of the embryo to individual blastomeres in the early cleavage stages of the egg. The beauty of some of the preparations in cell-lineage studies, especially, those which employ the silver nitrate technique, appeal greatly to the aesthetic sense.

Meanwhile the perfection of histological techniques and the compound microscope was ushering new advances in cytology. By 1882 mitosis had been observed and correctly described by Flemming, Strassburger and Von Beneden. A few years earlier, in 1875, O. Hertwig had explained and described fertilisation of the ovum, and by 1887 the brilliant researches of Von Beneden on *Ascaris* gave a complete picture of fertilisation.

These cytological discoveries logically led to the development of cell-lineage studies and have continued to be of profound significance for embryology.

Cell-lineage studies had only a limited role and are not generally included in current programmes of investigations in embryology. As a result of the cell-lineage studies the significance of the germ layers has diminished and in the context of the later developments in embryology the formation of germ-layers is only important for descriptive convenience, the distinction between the layers being morphological and not physiological.

Another event which helped the emancipation of embryology from the influence of the Haeckelian hypothesis was the initiation of "Entwicklungsmechanik" — by Wilhelm Roux in 1895. The application of causal laws and mechanical principles in physical

sciences had been crowned with phenomenal success in the nineteenth century and the more progressive biologists like His and Roux in tune with the spirit of the age aspired to understand the causal factors in development by the application of the physical laws and experimentations.

In one sense, the work of Wilhelm His and Weismann's concept of determinants were responsible for stimulating experimental analysis of development. The former attempted to explain embryological processes like neurulation in terms of physical forces, and devised experiments with models to corroborate his hypothesis. It is, however, Roux that is regarded as the founder of experimental embryology, for he experimented on living embryos. In a classical and oft quoted experiment he plunged a hot needle into one of the two blastomeres on the two-celled stage in the development of the frog to determine the potentialities of the individual blastomeres. He defined as the aim of the new discipline in embryology the analysis of the causes, forces and factors operating in the formation of the organism.

Modern or causal embryology is marked by three phases of growth, (1) The pre-Spemann era which mostly covers the later years of the nineteenth century (2) The Spemann era extending from about the beginning of the present century till the second World War and (3) Post-Spemann period which includes the war and post-war years.

During the last decade of the nineteenth century experimental embryology grew into a healthy sapling through the labours of a band of enthusiastic pioneer workers like Wilhelm Roux, Pflüger, Driesch, Hertwig, Morgan, Loeb, and Herbst. Their work illustrates that investigations in embryology had definitely shifted their mode of approach from the historical to the analytical, and as Paul Weiss[9] said, 'dynamic causation and not historical seriation became the thread along which the embryonic events were lined and linked up'. This view-point was in a certain measure due to medical men and physiologically inclined biologists undertaking the investigations of embryology. The historical viewpoint in embryology, as explained by Paul Weiss[10] was represented by naturalists, whereas dynamic causation was the view point of medical

9. Weiss, P. 1939. *Principles of Development,* p. 120, New York.
10. Weiss, P. 1939. *Vide supra.*

men and physiologists who could hope to cure the ailments of patients only by analysis of immediate causes.

The main concern of most of the embryological investigations in the last decade of the nineteenth century was the problem of mosaic *versus* regulative development, a distinction which is not valid at the present day. We are accustomed to the concept of determination and the fixing of the fate of parts of the embryo at a definite time. But Weismann and Wilhelm Roux held that the fates of an embryo were all fixed to begin with and development proceeded by a mosaic-like distribution of potencies to the cells in segmentation. The methods of approach to the problem included, apart from observations on the normal development of eggs, observations on the development of isolated blastomeres, defect experiments, the alteration of the environment of the embryo etc.

Contrary to the view of Roux and Weismann, Pfluger and Dreisch held that development was of the regulative type. The pressure experiments of Pfluger, and Driesch's experiments with isolated blastomeres of sea urchin egg are familiar to students of embryology.

The achievements of the pre-Spemann period were mainly in the experimental techniques which were devised. Besides the experiments mentioned already, Herbst's experiments on the induction of exo-gastrulation in sea urchin gastrula (1892) Loeb's early experiments on inducing artificial parthenogenesis belong to this period. The significance of Herbst's experiments has had increasing importance with the passage of years. Experiments in the separation of the blastomeres of the sea urchin by using calcium-free sea water were carried-out by Herbst in 1900.

As regards the theoretical contributions of this period, one of course is the partial clarification of the issue relating to mosaic *versus* regulative development. Besides this, the concepts of prospective significance and prospective potency were contributed by Driesch. His vitalistic theory of entelechy is now only a matter of historical interest, but the investigations which led to it are quite fundamental as Needham[11] has explained. The term prospective significance indicates the actual fate of any part in the

11. Needham, J. 1950. *Biochemistry and Morphogenesis*, p. 100, Cambridge.

original egg. Driesch made the great discovery that the fate of a such part was not exhausted by its prospective significance but it was changeable. Prospective potency signifies the collection of possible fates of such a part. In normal development only one of these possibilities is constantly realised. This is prospective fate. In abnormal development quite a different result may be seen. This feature of multiple possibilities of potency has been termed pleuripotency.

Lastly, we have to note that *Entwicklungsmechanick der organ* which is devoted to the new embryology marks this new era.

Spemann Era

Development, we defined as physiology of ontogeny, but it differs from physiology as usually understood in two ways. Firstly the temporal factor or *'duree'* is very important in development and has much greater significance than in ordinary physiological events. Every embryological event, we see, is the result of the past and preparation for the future. The web of development is woven by the fates, past, present and future—the three sisters of Greek mythology who seem to enmesh every embryological event. Viewing every embryological event as a physiological event, we must remember that the latter is only a *section in time* of the whole physiology of development. The second difference between ordinary physiological events and physiology of ontogeny is that the latter is progressively complex as a rule and not reversible and cyclic. Time is implied in the order of progressiveness but complexity not necessarily. I have digressed to elaborate these points, chiefly to emphasise that development is a dynamic process in which both temporal and spatial factors are important.

We study the physiology of an organism with reference to both its external *milieu* and internal *milieu*. A similar approach should be followed in the study of developmental physiology. In the pre-Spemann era the techniques and experiments related to only the external environment. There were no attempts to investigate the mutual influence of the parts within the embryo and how this might shape developmental events. In the experiments with isolated blastomeres, the aim was to see how each of these would develop by itself and not how it influenced another part of the embryo.

To Spemann is due the credit for initiating the experimental investigation of intrinsic factors of development. The Spemann

era is characterised by the investigation of the influence of one part on another in the embryo, by the employment of micro-surgical devices and by grafting experiments.

But it is not to be understood that during this period the investigation of the extrinsic factors influencing development had been given up. In 1900, as mentioned already, Herbst demonstrated that isolation of blastomeres of the sea urchin blastula occurred in a calcium-free medium of sea water. Loeb continued his experiments on artificial parthenogenesis. In 1901 he induced development without cleavage in *Chaetopterus* by treatment with KCl and other salts as well as dilute HCl. During the first decade of the century F. R. Lillie investigated more fully the phenomenon of development in embryos of *Chaetopterus* after experimental suppression of cleavage. The experiments for the induction of cyclopean eye were carried out by Stockard first in 1909. Experiments in the extirpartion of the polar lobe in *Dentalium* were also carried out during this period. The apparent lack of regulation in the frog's egg which Wilhelm Roux's experiment seemed to show, was reinvestigated by A. Brachet, and in the light of Spemann's work it was shown that the development of the frog was really regulative and mosaic, and that regulation depended on the influence of the organizer region. It became apparent that defect experiments and isolation experiments alone could not be conclusive, but only suggestive and have to be supplemented by the new techniques of translocation and recombination and grafting.

Most of Spemann's experiments, which are familiar to students of zoology, were carried out during the first decade of the present century. The amphibian egg, for evident reasons, became the chief object of embryological investigations as *Drosophila* has been in genetics. Between 1901-1907, Spemann and his pupils carried out a series of experiments with their technique of glass needles and grafting. The experiments established the principles of induction, competence and double assurance and demonstrated the possibility of a diffusible substance released by the optic vesicle inducing lens fromation in the overlying ectoderm. By the classic constriction experiments carried out in 1902 and 1903, Spemann demonstrated the equipotentiality of the cleavage nuclei and that some factor in the region of the prospective blastopore was essential for differentiation. Later in 1924, Spemann and Mangold, grafted the dorsal lip of the blastopore and showed that

the chorda mesoderm invaginated and organized the formation of the neural axis of the embryo.

At this stage Bautzman, Holtfreter and a few others started the investigations on the properties of the living, dissociated, crushed, boiled, killed and extracted samples of organizer material. Their experiments showed that the neural inductor is a moderately heat-stable chemical substance that does not depend on the integrity of the living tissues for its biological properties. It was further shown that the occurrence of the organiser substance was not limited to the dorsal lip of the blastopore but was of wide occurrence without, however, manifesting its influence in the normal course of events.

These experiments laid the foundation for the next era in embryology, the post-Spemann period. Already during this period, Holtfreter, Woerdman and Needham pursued the investigation of the chemical nature of the organiser, and the latter investigator[12] published in 1932 the three volumes of Chemical Embryology.

Thus the advances in experimental embryology during the first three decades of the present century were scarcely less important than those in genetics.

From the theoretical point of view, the work of S. Horstadius[13] on sea urchin development was of great significance. By combining the technique of calcium-free sea water of Herbst and the microsurgery of Spemann, by crossing the old and new techniques, Horstadius[14] inaugurated in 1928 a new era of experimental work, which with its roots in Herbst's experiments on the influence of lithium ions on sea urchin development, had its ramifications in Lindahl's[15] work in 1936, and affords support for the well-known Runnstrom's[16] theory (1928) of a two-gradient interacting system in sea urchin development. Costello[17] points out that this theory is a special example of the theory of axial gradients propounded by Child.

12. Needham, J. 1931. *Chemical Embryology,* 3 Vols., Cambridge.
13. Horstadius, S. *Biol. Rev.* 14. 132.
14. Hōrstadius, S. 1928. *Acta. Zool,* 9. 1.
15. Lindahl, P. E. 1936. *Acta Zool.* 17, 179.
16. Rünnstrom, J. 1928. *Acta. Zool.* 9, 365.
17. Cotsello D. P. 1949. *In Survey of Biological Progress,* Vol. 1, (ed. Avery, J. S.).

Two more achievements of this period are the development of Vogt's technique for marking the presumptive areas of embryos and the axial gradiant theory of Child. The latter was the first comprehensive hypothesis which attempted to account for the qualitative differences along the axes of the embryo. It found a specially helpful application in explaining the phenomenon of regeneration.

Meanwhile, embryology was showing indications of developing an alliance with genetics, particularly through the development of physiological genetics by Goldschmidt. This alliance fully materialised in the early years of the post-Spemann period.

The over-all achievements of the Spemann period are as follows:—1. Continuation of the experimental technique initiated by Roux, Herbst, Loeb, Driesch in the XIX century. 2. The rise of the Spemann school—and the development of the new hypothesis —the theory of organisers. 3. The formulation of the theory of axial gradients and the concept of fields. 4. Initiation of the pursuit of the chemical approach in embryology. 5. Indications of an alliance with genetics. 6. The starting of *Journal of Experimental Zoology* in 1904. 7. Decline in the significance of germ layer. 8. Resolution of the difference between mosaic and regulative modes of development. 9. Replacement of the old concept of specific organ-forming substances in a mosaic pattern by the idea of presumptive areas and fate maps. 10. The sublimation of the recapitulationary idea into the concept paedomorphosis began during this epoch. This, however, has no direct bearing on our present topic.

The Post-Spemann Era in Modern Embryology

During the first two decades of the present century the Spemann school of experimental embryology, employing biological methods of investigation, established the theory of organisers. During the third and fourth decades, the period between the two wars, the chemical nature of the inductor and its action became the focus of investigation by a number of workers like Needham and Waddington in England, Holtfreter in Germany and Barth in the United States. The solution of the problem which appeared at one time to be within grasp escaped, and the investigations served only to reveal the complexity of the problem.

However, these attempts to trace morphogenetic processes like induction to their biochemical predecessors helped to establish an

intimate union between embryology and biochemistry, which is well illustrated by Needham's encyclopaedic work—*Biochemistry and Morphogenesis* (1942), and Brachet's *Embryologie Chemique* (1944). It seems as though the war years helped the birth of biochemical embryology, for it was also during this period that, Woerdemann and Raven in Netherlands, in spite of the German occupation of the country and the oppression and the starvation of the people that followed, planned and carried out embryological investigations, the results of which have been published as a monograph in Experimental Embryology, in the series—"Monographs on Progress of Research in Holland During the War Years 1940-45". Raven's work on the development of *Limnaea* has set a new objective for embryological studies. Starting with the concept that developmental processes may be regarded as changes in a physico-chemical system, he has tried with the aid of cytochemical methods to unravel the chemical composition of the egg, and trace the physical and chemical changes, in short to present a complete picture of the chemical embryology of *Limnaea stagnalis.*

Contacts between embryology and chemistry, there have been ever since Herbst tried in 1892 to modify morphogenesis by changing the chemical composition of the embryo of the sea urchin through the administration of chemical agents like lithium to the surrounding medium. But there were no concerted efforts to investigate the chemical changes in relation to developmental processes. The three volumes of chemical embryology by Needham[18] summarise exhaustively all that was known till 1931 regarding the composition, nutrition and metabolism of embryos, but contain no references to morphogenetic processes. The same year also saw the successful experiments by Holtfreter in effecting induction with dead organiser tissue, and this success lured embryologists to the biochemical approach.

With this new approach, embryology has become a more dynamic study of development. Its objective, as defined by Gustafson and Kinnander,[19] is to map the biochemical and cell-physiological processes in embryos of different stages of development and to follow the manner in which these molecular processes are translated into morphological terms at the level of cells, tissues, organs and whole organisms.

18. Needham, J. 1931. *Chemical Embryology,* 3 Vols., Cambridge.
19. Gustafson & Kinnander, 1956. *Exptl. Cell Research,* **11**, 36.

Those inclined to view with suspicion this new alliance of embryology and biochemistry may remember that outcrossing in scientific disciplines is always beneficial and productive and that biochemistry as Baldwin[20] said "is perhaps more a way of thinking, a way of attacking biological problems than a mere subject".

The progress in this new approach has been considerably promoted by the improved precision instruments, cytochemical and other techniques and also by the advances in biochemistry, particularly protein chemistry and enzymology, and also in immunology and microbiology. Besides the common 'light microscope', the phase-contrast microscope, the polarising microscope, the electron microscope, microspectrophotometry in the visible as well as the ultraviolet have all helped the recent progress in embryology. Ultramicro-methods of analysis and manometry, particularly the techniques of the Carlsberg school of microtitration, and cartesian microrespirometry, have helped investigations at the level of the blastomere, and other techniques unimagined before have helped the isolation of component structures. The micromanipulator, the radioactive tracer technique, the new staining techniques including those for enzymes and some of the amino acids in the egg, chromatographic and electrophoretic methods, freeze-drying techniques, immunological methods, besides the old ultracentrifugation and tissue-culture methods have all been pressed into the service of embryological investigation during the last ten years. By time-lapse cinematography, studies of morphogenesis with reference to gastrulation in swimming sea urchin larvae have been made by Gustafson and Kinnander.[21]

The increasing importance of the new approach in embryology is reflected not only in the treatises already mentioned and monographs and several original papers but also in the new journals bearing on the subject which have been published in recent years. The *Experimental Cell Research, Journal of Embryology and Experimental morphology,* both of which are international, and the *Embryologia* mark the new period in embryology just as the *Arch. Entwicklungsmech. der organ* (1887) and *Journal of Experimental Zoology* (1904) inaugurated respectively the pre-Spemann and Spemann eras in embryology.

20. Baldwin, 1956. In '*What is Science*', London.
21. Gustafson and Kinnander 1956. *Exptl. Cell Research,* **11**, 36.

The problems confronting the investigator in embryology today are the same old problems but emphasis and techniques are different. The nature and action of the primary organiser, the question of equipotentiality of the cleavage nuclei, the manner or origin of the cytoplasmic differences the mechanism of morphogenetic movements, morphogenetic fields, mode, and time and nature of gene action, all these continue to be investigated with renewed zeal but the approach now involves new techniques and tools, and also the study of enzyme-systems, protein biosynthesis, amino acid metabolism, nucleic acids etc. The study of nuclear embryology is gaining importance. The over-all problem into which all these have to be integrated is of course the problem of differentiation.

Inductors

Embryologists, like Penelope, are always beginning afresh and at the same work. When the hope that the inductor substance would prove to be a chemical substance and that the induction phenomenon is something like a hormone action met with disappointment, attention was turned again to the organisers and the question was asked whether the induction stimulus was specific or non-specific and its action direct or indirect. The inductor property could be induced in tissues which normally did not possess it, and it appeared that there was a snag in the experiments producing artificial induction. The superficial layer of the host tissue had to be injured in grafting, leading to sub-lethal cytolysis which, it was suggested by Holtfreter,[22] might liberate the host tissue's neural inductor. Morphologists, to quote Needham,[23] "retired to the celebrated last redoubt of baffled biological thinking, unspecified stimulus". Others like Brachet[24] held on to the view that a specific biochemical or biophysical stimulus passes during induction. Niewkoop[25] has published a number of papers in which he developed the hypothesis that the inductive action has the characteristic of field phenomena.

Several new and interesting experiments relating to induction have been carried out in recent years. Alcohol extracts of adult

22. Holtfreter, J., 1944. *J. exptl. Zool,* 95, 307.
23. Needham J. 1955. In *Annual Review of Physiology*, Vol. 17, p. 38.
24. Brachet, J., 1949, *Ann. Soc. Roy. Zool. Belg.*, 80, 25.
25. Nieuwkoop, P. D., 1952. *J. Sxptl. Zool,* **120**, 1.

bone, injected into muscle induces there the formation of cartilage and bone cells. Toivenen[26] and Saxen found that alcohol denatured bone extract on implantation to ectoderm acted as a purely mesodermal inductor, not even a single nerve cell being produced. Such specificity points to direct induction and not indirect induction as the hypothesis of sublethal cytolosis would imply.

The induction of the embryonic axis has been viewed latterly as a stimulus-response mechanism in which the stimuli provided by various tissues and extracts of tissues evoke responses in the epidermis of the amphibian gastrula. The responses of the epidermis are classified according to the structures they produce, archencephalic, deutocephalic and spinocaudal. A fourth response of the epidermis is whereby only mesodermal structures are produced. Guinea-pig or rat liver preparations generally are used to induce archencephalic structures, guinea-pig kidney preparations for spinal inductions.

It has been suggested that there are at least two factors involved and some gradient distribution of the factors.

Brachet has for some years held the view that microsomes might pass from chorda mesoderm to presumptive neural plate and play a role in induction.

Recent investigations indicate that penstose nucleoproteins are chiefly responsible for specific induction. But, it seems, the pentose nucleic acid moiety may not be essential since almost complete removal of it by ribonuclease in extracts of pig kidney and rat liver does not change the inducing capacity of these extracts. (Barth[27])

In contrast to the general view that inductors are protein in character it was recently shown by Holtfreter[28] that killed tissues liberate substances like ribonucleoplroteins which can diffuse through agar or cellophane membranes and induce neurulization of ectoderm placed in contact with the membrane. But when a cellophane membrane is placed between normal inductor and the reactor, induction fails. For this reason Needham[29] remarked that

26. Toivenen, S. and Saxèn, L. 1955. *Exptl. Cell. Research, suppl.* 3, 346.
27. Barth, L. G. 1957. In *Annual Review of Physiology,* Vol. 19, p. 41.
28. Holtfreter, J. 1955. *Exptl. Cell. Research. suppl,* 3, 346.
29. Needham, J. 1955. In *Annual Review of Physiology,* Vol. 17, p. 40.

the effects of interposition of semipermeable membranes between inductor and reactor are enigmatic. Does this mean that the view that R. N. A. has a role in induction has to be rejected? Brachet[30] has very recently discussed this question and emphasised the idea that biochemical mechanisms underlying normal induction might be different from those at work when killed tissues or nucleoproteins etc., are used as evocators, and it is the integrity of the protein rather than that of the R.N.A., which is necessary for the normal evocation activity.

In this context the work of Niu and Twitty,[31] and Niu[32] has considerable importance. These authors have initiated a new and very promising approach to the problem of embryonic induction, using a new technique. In this the organizer tissue is explanted into a hanging drop of modified Holtfreter solution, and about a week later small pieces of ectoderm are introduced at a distance from the developing organizer. In ninety percent of the experiments induction is successful.

The investigations of Niu[32] have also revealed that more than one kind of inductor substance is involved and that 'young' ectoderm can differentiate even in the cell-free medium withdrawn from established cultures of inductors. Further, the medium has an absorption sprectum similar to that of nucleoprotein. This conclusion has received support from the results of chemical methods like dialysis, alcohol precipitations, colour tests and also enzyme studies.

Thus we are now more optimistic than before about the solution of the problem of embryonic induction. Barth[33] has remarked that if we accept the general trend of thinking that inductors are pentose nucleoproteins, we could wish for no better specific compounds as activators of specific nuclear genes whose visible effects constitute differentiation.

Proteins and Amino Acids in Development

A new feature of the embryological investigations during the last five years is the increasing emphasis on proteins and amino

30. Brachet, J. 1957. *Biochemical Cytology.*
31. Niu, M.C. and Twitty, V.C. 1953. *Proc. Natl. Acad. Sci. U.S.*, 39, 985.
32. Niu, M. C. 1956. *Cellular Mechanisms,* in *Differentiation and Growth,* p. 155, Princeton.
33. Barth, L. G. 1957. In *Annual Review of Physiology,* p. 52.

acids during development. This reflects, as Ebert[34] has pointed out, that the new embryology has as its ultimate aim the interpretation in molecular terms of the structural and functional relationships in differentiation during development. It is needless to dwell at length on the importance of proteins for a proper understanding of living organisms. Mulder, as early as 1845 said: "Without it (proteins) no life appears possible on our planet, through its means the chief phenomena of life are produced. Engels made a more dogmatic assertion by saying that 'life is the mode of existence of protein bodies'. If chemical embryologists of a previous generation did not lay so much emphasis on proteins, it was because of technical and other difficulties. In recent years the rapid strides made in the chemistry of amino acids and to some extent of proteins, the development of micromethods like chromatography, the availability of the radio-active tracer technique, electrophoretic analysis etc., have opened a new field of biochemical embryology.

The complement of proteins and other macromolecules in a cell is highly complex. There can be no doubt that during development there are qualitative and quantative changes in the complement of proteins molecules and in their association with other molecules and there should also be syntheses of specific molecules characteristic of the different cell types. One problem that confronts us is whether all these specific protein molecules are represented in the ovum, or are synthesized during cleavage.

The former view would imply that the egg should contain a very large number of specific protein molecules, which is very improbable. If syntheses were to take place, it would mean availability of a source of free energy for various synthetic processes, which may not be available at this stage. Barth and Barth[35] have suggested that the specific proteins of various cell types found in an organism are not synthesized individually, but might exist rather as few general precursor proteins or proteinogens. On this view, development would be a mechanism of the orderly activation of the proteins from proteinogens without the necessity for free energy.

34. Ebert, J.O. 1954. In *Aspects of Synthesis* and *Order in Growth*, p. 69, Princeton.

35. Barth, J. and Barth L. G. 1954, *Energetics of Development*, New York, p. 8.

Experimental evidence is available to show that embryos may contain proteins which the adult animal lacks. The serum of the foetal calf contains a new protein absent in the adult serum. The haemoglobin of the embryo is different from that of the adult.

Another interesting feature revealed by recent investigations is that the proteins necessary for an organ may appear long before the organ functions, and not in the future site of the organ or presumptive area but in other localities. Ebert[36] has shown that the synthesis of cardiac myosim is initiated in the chick during the early stage of primitive streak formation. Later when the latter structure is fully differentiated it is distributed throughout the epiblast but not present in the hypoblast. At the head-process stage it is restricted to presumptive heart areas. The same author has also shown that actin present in the adult heart is present in 12 day's chick embryo and one of its specific antigens is present even as early as 36 hours.

There has been a continued search for the role of pentose nucleic acids in protein syntheses. There is no doubt that R.N.A. is necessary for protein synthesis but we are not sure whether there is any absolute correlation between the two (Ebert).[38] There is considerable evidence in support of the hypothesis that R.N.A. granules are the site of protein syntheses, but there has not been sufficient substantiation for the biological properties like auto-duplication attributed to microsomes in the cytoplasm.

During oogenesis there is active synthesis of proteins and other molecules, probably also of direct transfer of proteins from maternal blood to the egg. In the oocyte no new proteins seem to be synthesized. During cleavage in which there is cellular multiplication but no over-all growth, the protein composition seems to be relatively constant but there is no actual synthesis during first half of each division cycle. At gastrulation the synthesis of R.N.A. and proteins is resumed.

Holtfreter,[37] Gustafson and Hjelte[38] and others have investigated the amino acids during development. Information about embryonic amino acids is of interest because of the possible light

36. Ebert, J.D., 1954. In *Aspects of Synthesis* and *Order in Growth,* p. 69.

37. Holtfreter, J. *etal* 1950. *Exptl. Cell. Research* 1, 453.

38. Gustafson, T., and Hjette, M.B., 1951. *Exptl. Cell. Research,* 2, 474.

it may throw on differentiation of embryonic processes. Gustafson and Hjelte[39] have shown that the concentration of nearly all the free amino acids in the sea urchin embryo rises to a peak just before the gastrula, then declines during gastrulation, evidently being used for protein synthesis.

Recently, Deuchar[40] has investigated the amino acids in the living tissues of *Xenopus leavis*. Among the interesting features recorded by him are (1) the development of high concentrations of free aspartic acid and glutamic acid in the morula followed by much lower concentration in the early gastrula (2) the greater concentration of aspartic acid in the animal half of the egg evidently connected with the more rapid turnover of the nucleotide in the animal pole cells than in the vegetal cells (3) the high total concentration of the free amino acids in the dorsal lip of the early gastrula (4) high concentration of aspartic, glutamic acids and glutamin in the dorsal lip (5) their concentrations in the dorsal half of the neurula and then in the brain (6) the resemblance in the free amino acid concentrations between embryonic tissue and larval tissues.

In an investigation by Ramamurthi[41] of the amino acids in the development of *Pila*, which is in progress, some interesting observations have been made like the synchronisation of tyrosine and pigmentation of the embryo on the 7th day.

As Ebert[42] has emphasised, development is not to be regarded as being no more than a chain of chemical reactions of which the net result is the localised synthesis of molecular species characteristic of a particular tissue. Molecular groupings and the ability of certain proteins to undergo reversible transformation from globular to fibrous form, either by end-to-end aggregations or by unfolding of molecule, these are important in the formation of complexes with spatial orientation. Ranzi[43] has shown the animalizing agents of the sea urchin egg causes a molecular transfor-

39. Gustafson, T., and Hjette, M.B. 1951. *Exptl. Cell. Research* 2 p. 474.
40. Deuchar, E.M. 1956. *J. Emb. Exptl. Morphol.*, 4, p. 327.
41. Ramamurthi, K. *J. Animal Morph. & Physical.* (In press).
42. Ebert, J. D. 1954. In *Aspects Synthesis & Growth*, p. 69. (Princeton).
43. Ranzi, S. 1953. *Arch. Néerland, Zool.* **16**. 10. *suppl.* 92, and *Exptl. Cell, Research*, 3 *Sppl.*

mation from fibrous to globular form and the vegetalising agents stabilize proteins in the fibrous state. It has been suggested that such transformations may play a role in differentiation.

In the context of the role of proteins in development a brief reference to the mechanism of gastrulative movements may be made. Holtfreter[44] tried to explain gastrulation as primarily caused by local change of surface tension changes of certain cells. Modern cell physiology has discarded this hypothesis. Of the other hypotheses we may mention the concept of Paul Weiss[45] who interprets the nature of the affinities between like and unlike cells in immunological terms. The complementariness or otherwise of cell surfaces may be regarded as based on molecular configurations projecting from them, and as similar to antigen-antibody relationship.

The role of proteins in the process of differentiation has been stressed by investigations during the last five years. As mentioned already, these recent studies show that not only do new proteins develop with time and become localized in the embryo but that inductors of various parts of the nervous system are closely associated with pentose nucleoproteins. Further and continued efforts in the investigations of proteins during development will help in understanding the intricate mechanism of development. Limitations of time do not permit me to review the investigations on the role of proteins in regenration and regulation.

Nuclear Embryology

(a) *Role of nucleus in differentiation*:

Generally speaking, it appears, the geneticists have claimed the nucleus as their monopoly to the exclusion of the cytoplasm, and the embryologists have concentrated on the cytoplasm to the exclusion of the nucleus in their investigations. It is only in recent years that geneticists have been exploring the possibility of a hereditary role by the cytoplasm, chiefly due to the investigations of Sonneborn, Ephrussi *et. al.* Let us not forget that nucleus and cytoplasm constitute a single entity or system. A nucleus without cytoplasm, a cytoplasm without a nucleus are both unreal.

44. Holtfreter, J. 1944. *J. Exptl. Zool.*
45. Weiss, P. 1953. *J. Emb. Exptl. Morphol.* **1**, 181.

Embryologists for several years have tacitly assumed that the realisation of nuclear factors happens only in later stages of development. As the nuclei come to be located in non-identical regions of the cytoplasm, differentiation results. This means that the nuclei have not undergone any change during development while the cytoplasm becomes increasingly heterogeneous.

Earlier investigators in the nineteenth century held a different view of the role of the nucleus in development. Influenced by the germplasm theory of Weismann, it was supposed that each blastomere finally came to receive only one kind of determinant. In other words a nuclear differentiation and segregation occurs synchronously with cleavage. In subsequent years experimental disproof became available by the experiments of Pfluger, Dreisch and Spemann. The classical experiments of Hertwig and Spemann on the early stages of the amphibian embryo showed that the nuclei present in cleaving eggs are totipotent, show no specificity and can continue to control the process of normal development when transplanted from one part to another. Seidel by destroying nuclei in the egg of *Platycnemus* by ultraviolet has shown that up to 128-cell stage, the intact nuclei are capable of replacing by mitoses those destroyed, and development proceeds normally. These and other experiments showed that cells with different nuclei show the same behaviour and cells with the same nuclei can show different behaviour depending on the cytoplasm.

So attention was all directed to the cytoplasm and the functioning of the nucleus being possible under the influence of the cytoplasm. The effect of cytoplasm on the nucleus is illustrated in germ-line track of *Ascaris*.

The question of the role of nucleus in differentiation, regarded before as settled, has been reopened very recently and posed as follows: Does cell-differentiation involve irreversible changes in the nuclei ? Are the nuclei, say of muscle cells, irreversibly specialised so that they can participate only in the synthesis of myosins and associated substances, or is the seat of this specificity of synthesis a function of the cytoplasm, the nuclei remaining genetically inert during development, or do irreversible changes take place in both the nucleus and cytoplasm or on neither ? Again are there any genetic entities in differentiated cells determining cell types ? If there be any, where are they located in the nucleus or cytoplasm ?

According to Lindahl[46] the micromere quartette of the sea urchin embryo undergoes at 16-32 cell-stage a reduction division producing haploid micromeres in the otherwise diploid embryo. A similar condition has been observed in mesenchyme cells of the tail tip of frog tadpoles. These results indicate that somatic reduction may be involved in the differentiation of mesoderm.

Biochemical variations among somatic nuclei have been reported by some authors. The nuclei of erythrocytes of birds contain haemoglobin lacking in other tissues. Biochemical data demonstrate that there are functional enzymatic differences among somatic nuclei.

The recent investigations by Briggs and King[47] have a very significant bearing on the problem of differentiation. King and Briggs[48] developed a method for transferring nuclei of embryonic cells into enucleated egg of *Rana pipens*. They have carried out a series of investigations. In the recent experiments endoderm nuclei of the late gastrula were transplanted into the enucleated egg. The transplantation tests show that the nuclei retain the ability to participate normally in cleavage but are usually restricted in their potentiality for differentiation of neural axis and other ectodermal derivatives ensues by induction. In others, development stops before any neural structures appear.

Other experiments show that at later developmental stages there is a loss in the capacity of these nuclei to enter into cleavage of egg cytoplasm. These experiments suggest a progressive specialisation of nuclear function during cell-differentiation. These authors have still further extended their investigations. In these, the nuclei of endoderm cells taken from the floor of the anterior midgut at different stages of development were transplanted into enucleated eggs of the frog *Rana pipiens*. When the nuclei were from the late gastrula, the majority of the recipient eggs cleaved and developed into partial or complete blastula. Although these were normal in appearance, they usually displayed pronounced abnormalities in later development. In some cases gastrulation was completed and development was arrested later. In the arrested

46. Lindahl, P. 1953. *Exptl. Cell. Research*, 5, 416.
47. Briggs and King, R. 1954. *J. Emb. Exptl. Morph.* 2, 73.
48. King and Briggs.

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embryos there were pronounced deficiencies of ectodermal derivatives.

When the endoderm nuclei were derived from the mid-neurulae, the proportion of recipient cleaving eggs was reduced and the development of resulting blastulae was more restricted. The majority were arrested in blastula or early gastrula stages. The remainder displayed abnormalities.

In the case of endoderm nuclei of the 'tail-bud' embryos the capacity to elicit cleavage in the recipient eggs was reduced still further.

From these experiments the authors conclude that endoderm nuclei undergo stabilized or irreverisible changes during differentiation. These changes appear to restrict first the ability of the nuclei to promote the formation of ectodermal and ectomesenchymal structures. Later the capacity to promote gastrulation and chordamesoderm formation apears to be lost and eventually the endoderm nuclei appear to lose the ability to elicit cleavage in egg cytoplasm.

These experiments show the possibility of a nuclear differentiation concomittant with differentiation and also of a causal connection between the two. Barth[49] has pointed out that as a result of these important experiments we may look forward to a time when the nuclei of various cell types will be proved to be different from another and that we will be able to speak of genetically different strains of cells. These different strains, as suggested by this author, would arise at first as a result of cytoplasmic localization in the egg and later embryonic inductions stimulate nuclear differentiation.

As pointed out already, there is an increasing realisation of the importance of nuclear studies in embryology. Cytology and embryology are twin disciplines. In the study of the reproductive cells, fertilisation, parthenogenesis and cleavage, it is impossible to draw the line between cytology and embryology.

But in the belief that the genes control only the later developed and more superficial characters of animals, and that development is controlled not by the nucleus but by the cytoplasm

49. Barth, L.G. 1957. In *Annual Review of Physiology*, p. 52.

only, the tracing of developmental events including the control of differentiation stopped outside the nucleus in embryological investigations till recently.

The work of Briggs and King,[50] as we saw, emphasises the importance of investigating the nucleus and what it does during early development. We may now speak of 'nuclear embryology' in view of the increasing number of papers on the subject and the brilliant technical achievements.

Another approach to nuclear embryology is by Horstadius[51] *et.al.* who injected D.N.A. from the same or related species into the eggs and have also studied the results of allowing the eggs to develop in sea water containing it. These experiments have shown that in many cases heterogenous D.N.A. arrested development.

New light on the activities of the nuclei during cleavage has come from the investigations of Swann and Mitchison[52]. These authors have analysed mitosis in the eggs of sea-urchin *Psammechinus mitiaris* by polarised light. By an analysis of the changes in birefringence in the cytoplasm of sea urchin eggs, it is found, certain structural changes are brought about by release of catalytic substances which the authors have termed "structural agents". The cortical changes at cleavage are also brought about in the same way, and the changes at fertilisation are caused by the release of structural agents from the head of the fertilising sperm. It is also suggested that these substances are either recondensed on the chromosomes, or synthesized afresh by them at some time in prophase in readiness for the next mitosis. Thus there is a controlling cycle for the whole mitotic process in which metaphase and interphase are focal points. Swann and Mitchison[53] have also examined a large number of other cyclic changes associated with mitosis chromosomes like cytoplasmic viscocity, cytoplasmic refractive index, respiration, quantity of SH- groups etc.

This interesting hypothesis of release of structural agents by chromosomes and of the relation of mitosis to cleavage is of special significance to the embryologist. The cleavage of enucleated eggs,

50. Briggs and King, 1957. *J. Morph*, **100**, 269.
51. Horstadius, *et al. Exptl. Cell. Research*, **6**, 440.
52. Swann, M. M., 1952. In *Symposia. Soc. Exptl. Biol.* **6**, 89.
53. Mitchison, J. M., & Swann. M. M. 1952. *Vide supra*,

which is sometimes regarded as a case of autonomy of cytoplasm seems to be due to nuclear material released by the break-down of the germinal vesicle at maturation.

(b) *The nucleus in relation to protein synthesis*:

That active protein synthesis on a large scale is involved in development and growth is generally accepted. The site of protein synthesis is recognised to be in the cytoplasm in relation to the R.N.A. granules. The question arises whether the nucleus has any role at all in protein synthesis. Due to the long neglect of the study of the role of the nucleus in embryological studies, we have had so far only inconclusive and fragmentary knowledge of intranuclear phenomena that might be related to protein synthesis.

Caspersson[54] put forward a scheme of intramolecular protein synthesis according to which proteins of a basic type are produced in the nucleous associated heterochromatin of the chromosomes, and later accumulate to form the main bulk of the nucleous. From the nucleolus these basic proteins diffuse outward to the nuclear surface where an intense production of R.N.A. takes place. Pollister[55] would interpret this as the appearance of microsomes.

But we have not had sufficient evidence so far, for such precise functions of the heterochromatin or nucleolus or the actual flow of the material from the latter towards the nuclear surface. Though there is correlation of nucleolar changes with protein synthesis, nucleolar size has not been shown to be a measure of relative protein synthesis.

Pollister[55] has recently put forward an interesting hypothesis on experimental evidence of the study of protein synthesis in the liver cells of rats. Protein is often rapidly produced as the substrate for specialised cells like muscle fibre skin cell etc. or it may be stored as zymogen granules, yolk etc. Every cell has to synthesize not only the specific proteins but also proteins for replacement or increase of the intrinsic enzyme proteins which make up the remaining bulk of cellular proteins.

The problem in development, differentiation as well as growth, is the understanding of the relationship of the nucleus to the

54. Caspersson, 1950. *Cell. Growth & Cell. Function,* New York.
55. Pollister, 1954. In *Dynamics of Growth Processes*, p. 33, Princeton.

specificity of each protein molecule. Pollister[56] suggests that we may assume that the gene in the chomosome actually forms the protein of the molecule which is responsible for the specificity. Pollister's scheme of the role of the nucleus in protein synthesis is as follows:—

1. The portion of the protein molecule formed by the gene and which is responsible for the specificity of the protein is called protein precursor. 2. Another assumption is that there is a nuclear and cytoplasmic stage in the history of each microsome. The intranuclear phase which may well be intrachromosomal is capable of self-duplication. 3. The intranuclear microsomes multiply and each takes up a specific protein precursor or, 4. The microsome then passes into the cytoplasm. It is then made of R.N.A. a complement of enzymes and a specific protein precursor. 5. Utilising soluble factor from mitochondria and amino acids, the microsome synthesizes maximum length of polypeptides and combines them with the nuclear protein precursor to form specific protein molecules. Once the supply of specific protein precursor is exhausted, the useful protein-forming life of the microsome is ended and the microsome breaks up to release the specific protein.

Pollister bases his hypothesis of protein synthesis on the experiments on liver cells of rats accompanied by cytological and chemical observations. Evidence from these experiments tends to show that the microsomes may be the main organs of protein synthesis.

Some evidence, it seems, has been accumulating for the extreme heterogeniety of microsomes. It is suggested that there may be as many as types of microsomal types as the number of specific proteins to be synthesized ultimately. This may not be likely or very necessary to assume.

Pollister[57] makes the microsome "the gene's transient representative" in the cytoplasm. But we have yet to know a good deal more about the composition and diversity of microsomes. In recent years the mitochondria have been intensely investigated and shown to constitute cyclophorase system. "In this system the different oxidases are so nicely balanced that at no point in the complex sequence of events is there even a temporary piling of

56. Pollister, 1954. *Vide supra.*
57. Pollister, 1954. *Vide supra.*

intermediates, the enzymes acting at the trace level of the substrate with an orderly type of oxidation". On the model of a cyclophorase system Pollister suggests that there may be a complex proteogenase system constituted by the microsomes for the synthesis of specific proteins. The proteinogens which Barth[58] conceives would then have to be looked for in the microsomes.

Allfrey et.al.[59] have very recently investigated the protein synthesis in isolated nuclei of calf thymus and demonstrated that protein synthesis can occur in both nucleus and cytoplasm.

I have dwelt on some of the new trends mainly to indicate the sign-posts in the progress of contemporary embryology.

Enzymatic Aspects of Differentiation

Genetical investigations in recent years have come to the conclusion that the genes which are responsible for inherited characters of an organism often act through enzymes, if not in one-gene-to-one enzyme fashion. Enzymes are very specific both as to the substrates on which they will act and as to the external conditions under which they will act. It is claimed by certain investigators that the specificity of enzyme activity might account for the particular types of differentiation occurring in the cells. Gradients, chemo-differentiation, presumptive areas and other concepts, it is suggested, will become more precise, if we could trace them to differences in enzyme concentrations. Prompted by this idea and helped by the new microchemical and micromanometric techniques, the detection of enzyme systems in cleaving blastomers and in different presumptive areas has been pursued.

But we must ask whether we should attach to differences in enzyme concentrations any more significance than we would to differences in yolk content or hyaline protoplasm in the blastomeres. Such of the enzymes as are adsorbed on the surfaces of cytoplasmic granules or other inclusions would be expected to follow the distributions of these granules and those present in the fluid hyaline portion would be distributed with this material. Can we induce alternations in morphogenesis by experimental alteration of the distribution of enzyme systems ? Modifications in the distribution of yolk and hyaline protoplasm as a result of centri-

58. Barth, L. J. and Barth, L. G., 1954. *Energetics of Development* 8.
59. Allfrey, V. G. and A. E. Mirsky 1955. *Nature,* **176**, 1042,

fugation does not affect morphogenesis as we know from the classic experiments of Morgan, Conklin and Lillie and others.

Another snag in the argument is that the gene-enzyme-character concept relates to characters and not to organization. It is misleading to equate development with development of characters and character patterns. The emphasis in embryology should be on the progressive increase of organization, for a mosaic of characters is not an organization.

However, the pragmatic value of the investigations of enzymes systems is not to be minimised, provided their causal significance is not exaggerated. Enzyme systems may indicate differential activities in development without having a causal significance in morphogenetic differentiation.

Intensive studies of embryonic enzymes have been made by several authors. Barth and Jaegar[60] have investigated the distribution and variation in the concentration of A.T.P. are in the development of frog. Gustafson[61] has made an excellent survey of the enzymatic aspects of embryonic differentiation with special reference to the sea urchin development.

The starting point for Gustafson's investigations is the classic experiment of Herbst, which showed the remarkable effect of lithium ions on sea urchin development in bringing about vegetalization or enormous hypertrophy of endoderm at the expense of the ectoderm.

In the development of sea urchin certain enzymes show a constant activity during development and these are non-mitochondrial; others which show a developmental rise are mitochondrial, the increase being related to the incrase in mitochondria. Gustafson[62] discusses the development of the sea urchin in terms of interaction between two antagonistic types of metabolism one of which is supposed to favour mitochondrial development whereas the other inhibits. Serological techniques reveal the formation of new specific components or antigens which may be water soluble or reside in microsomes. The origin of specific molecules and the

60. Barth, L. G., and Jaegar, L. 1947. *Physiol, Zool.* **20**, 133.
61. Gustafson, T., 1954. *International Review of Cytology*, **3**, 277.
62. Gustafson, T., 1954. *Vide supra.*

regulation of their spatial distribution is the basic problem of ontogenic enzymology.

In another place we presented Pollister's hypotheses. Differences in enzymatic properties of nuclei isolated from various organs have been demonstrated by Mirskey.[63] This means that enzymes are due to the activation of genes. Other investigators like Poulson,[64] Sonneborn[65] and Spiegelman[66] would regard differentiation as a rather cytoplasmic question. Sonneborn believes that the serological specificity of a differentiated tissue may be determined by the competition between population and serologically different plasmagenes. Spiegelman suggested that the plasmagenes are involved in the synthesis of various enzymes, and that differentiation results from the multiplication of different kinds of plasmagenes in different regions, conditioned by the amount of substrates in various parts of the embryo.

In all these concepts there is the desire to equate embryonic differentiation with the successive elaborations of particulate populations isolated from each other or superimposed in time and space (Gustafson)[62].

The assumption of autonomous cytoplasmic particles or plasmagenes is originally based on certain results obtained by genetic methods by Sonneborn, Euphrussi and others. Spigelman[66] discussed the mechanism of differentiation on the basis of the plasmagene concept. and considers that differentiation is the outcome of a competitive interaction between different enzyme-producing plasmagenes. Spigelman's experiments, which are based on enzyme adaptation in yeast show, as mentioned already, that a modification of the enzyme occurred against a constant genetic background. Gustafson and Runnström have pointed out that the term 'plasmagenes' should be reserved for cytoplasmic units, independent of genes, but which have continuity, mutability and whose entire cycle is confined to the cytoplasm. The "plasmagenes" of Spiegelman are gene products. Runnstrom[67] has remarked that it

63. Mirskey, A. E., 1951. In *Genetics in the 20th Century.*
64. Poulson, O. F. 1945. *American Naturalist,* 79, 340.
65. Sonneborn, T. M. 1951. *Cold Spring Harbor Symposia. Biol.,* 16, 483.
66. Spiegelman, S. 1948. *Symposia. Soc. Exptl. Biol.* 2, 286.
67. Runnström J., 1952. In *Modern Trends in Physiology, and Biochemistry.* (ed. Barron), p. 73.

is more a question of terminology as to whether the replicating gene products should really be designated as "plasmagenes".

Brachet has recently discussed the plasmagene hypothesis as in relation to differentiation and points out that there is no factual evidence as yet in its favour, although it cannot be rejected, pending further experimental investigation. But the investigations by Briggs *et al*[68] cast considerable doubt on the existence of true plasmagenes in the eggs. If 'plasmagenes' exist, we have to look to gene initiated products as pointed out by Waddington[69] (1956).

It is questionable whether there are any non-gene initiated cytoplasmic particles which satisfy the criteria of a plasmagene, other than plastids, virus and central apparatus. Barth[70] in referring to the work of Briggs and King has remarked that it may well be that the concept of plasmagenes will no longer be necessary.

Differentiation is not equivalent to the controlled production of enzymatic patterns. These concepts have some pragmatic value, provided it is remembered that they refer only to some particular aspect of differentiation process.

The success of the particulate hypothesis in gentics seems to have influenced some of the embryological hypotheses which invoke particulate factor populations to account for differentiation. These hypotheses, it appears to me, overlook that differentiation in embryonic development is not mere differentiation of characters but involves an integration into a progressive increase of complexity of organization.

Moog[71] has investigated the enzymes in the developing chick. As in the case of the protein biosynthesis the appearance in the embryo of some of the enzymes investigated long before they are required to function is noteworthy.

CONCLUSION

Limitations of time permit only a passing reference to various other currents in the new embryology. The role of the genotype in development continues to be investigated. The method adopted

68. Briggs *et al* 1957. *Vide supra.*
69. Waddington, C.H. *Principles of Embryology,* London.
70. Barth, L.G., 1957. In *Annual Review of Physiology,* **19**, **52.**
71. Moog, F., 1952. *Ann. N. Y. Acad. Sci.,* **55**, **57.**

is to determine the effect of a mutant gene by comparison with the effect of its normal allele. This means the determination of the phenotypic difference at the stage of development, when it can be first recognised. This pushing back the analysis of phenotypic difference to a stage in development does not necessarily reveal what the gene does. Much work has been carried out with the technique of transplantation of piece of tissue of one genotype into a host of another to study the 'gene hormones' which determine the reaction of the transplant. But it is not so much the genetical alliance as the biochemical alliance which characterises the embryology of to-day. The concept of gradients and fields has also continued to receive some attention in recent years. The term field was used for the first time by Spemann in 1921, but has since been widely used. It must be confessed that the term field is still a symbolic one with no precise definition in terms of space, time and energy. It has been suggested that it might be electrical, and that the data on electrical fields might be employed to define more exactly the term field in the sense used by the embryologists. But there are several technical difficulties in the method of approach to the problem of the role of bioelectrical potentials in living cells. All attempts to arrive at a physico-chemical explanation of fields are supported so far by little critical evidence. But the concept of field has been useful in indicating that the analysis of morphogenetic mechanisms must be pushed back to the very commencement of development and that we have to keep open our minds to receiving help from other scientfific disciplines.

Child's concept of gradients as stated before has the distinction of being the first attempt to frame a comprenensive theory to explain qualitative and pattern developments in terms of quantitative localised regional differences.

The serological approach, the use of antimetabolites, and the use of radioactive isotopes are procedures of technique which are of great value in some of the current embryological investigations.

We have made a rapid survey of the development of embryology indicating its bearings at different periods of development. The germ of embryological science found in the work of Aristotle had a long resting period like the oocyte, till it was fertilised and activated by the observations of Malpighi, Harvey and Wolff. It was next determined for new potentialities (the presumptive fates) by von Baer and ushered into an era of accelerated development by the gastrulative effect of the evolution theory. Later

it was 'inducted' for dependent differentiation by the experimental methods of Roux, and is now undergoing self-differentiation very rapidly in several directions. Like the phenomenon which it treats, the science of embryology has shown a progressive increase in the complexity of its organization from the time of Aristotle to the present day. Casual observations, comparative embryology and concept of germ-layers, descriptive embryology with the recapitulation theory, *Entwicklungsmechanik,* chemical embryology, biochemical embryology and dynamics and energetics of development — these are the mile-stones in the progress of the embryological science.

Present-day embryology is an intricate web of techniques and concepts emanating from all scientific disciplines and also metaphysics. The zoologist who aspires to embryological research cannot afford to remain content with microtomy and the classical staining procedures, but has to become familiar with the techniques and concepts of several branches of knowledge.

I am aware that I have not emphasised the problem of 'differentiation in development'. This term has been used with different connotations. Differentiation in embryology is the increase in complexity of organization, and the mechanism of differentiation is the sum-total of all the changes,—'the integrated whole of the changes between one stage and the next'. The most stimulating discussion of the problem is by Paul Weiss[72] who has put forward a hypothesis for the production of structural order in differentiation in molecular terms. This implies "unscrambling and selective localization of molecular populations, setting the stage for consecutive reaction chains". Any embryologist who has reflected on the problem of development will appreciate the statement of Paul Weiss that "differentiation is not something that should or could be defined in our present state of ignorance and conflicting opinions", and that "the study of differentiation stands to make much faster progress if instead of looking for sweeping generalizations or insisting on generalities we first dissassemble the complex process into its constituent components". At the present moment embryologists seem to be casting about for hypotheses. It would be better to wait till we have more facts, or till an intuitive genius looks at facts with insight. It requires a new vision and

72. Weiss, P., 1953. *Vide supra.*

imagination to put forward a new hypothesis. The present emphasis on protein biosynthesis during development is a step in the right direction. Mention must be made also of the stimulating study by Barth and Barth[73] on the energetics of development in which they have attempted to trace how energy is transformed during development to produce cellular differentiation and growth. But the caution is necessary that the present, pre-occupation with biochemical approach to embryology does not imply that biochemistry by itself will suffice to explain the phenomenon of development. How biochemical processes are organized in space during development is difficult to grasp. Most biochemistry is a description of time sequence of chemical reactions between reactants in solution. The space variable barely comes in. Reactions in the cells are organized in space as well in time. Rarely do they come close as in the muscle, the biochemistry of which we know a good deal.

Throughout I have emphasised the idea that the organism is a whole, and developmental events must be integrated into it. This is not the occasion to refer to metaphysical aspects but we must not forget that, as Agar[74] has pointed out "it is not only legitimate but necessary for the biologist to include in his explanatory schemes factors which are unnecessary for the explanatory schemes of the physicist — namely such concepts as memory, anticipation, purpose, final causation, in a word, perception". Sinnott[75] points out that the biologist as well as the philosopher should widen his horizon.

The wonder of development will continue to remain. In tracing development from any approach let us not forget that development irreversibly progresses to the goal of producing the organism and at higher levels an organism with hopes and aspirations and urges. Are all these immanent in the ovum, or merely the result of physicochemical reactions? And if the action of genes can result in the development of pattern and organization, the genes cannot be a haphazard aggregation; the genotype itself must be organized i.e. an organic whole. When we come to understand better the progressive increase in organization during

73. Barth, L. J. and Barth, L. G., 1954. *Vide supra.*
74. Agar, W. E., 1951. Cited in *Biology of the Spirit*, p. 14, London.
75. Sinnott, E. W. *Biology of the Spirit*, p. 14, London.

development we may get a better insight into the organization of the genotype. There should be an embryological approach to genetics to complement the genetical approach to embryology. Scientific embryology is moving towards the ultimate goal not of *form and matter,* but as Needham[76] said, *organization* and *energy.* But let us not speculate whether we will ever understand development even if we know everything about it. Knowing is not understanding. The future need not bother us for,

> "To travel hopefully is a better thing than to arrive".
>
> [R. L. STEVENSON]

It would be fitting to conclude a review of the development of embryology with the following lines from Shelley :

> "The one spirit's plastic stress
> Sweeps through the dull, dense world, compelling there,
> All new successions to the forms they wear"

76. Needham, J. *Biochemistry and Morphogenesis,* xxvi, Cambridge.

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Notes on the Distribution and Seasonal Variations of Marine Borers of the Madras Area

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I. *Introduction*

Though attention has been paid to the record of wood borers from the taxonomical point of view, very little information is available regarding the species of borers active and the extent to which each species is responsible in the total destruction of timber at various sites in the same locality, their concentration during the different periods of the year and the ecological conditions under which they lived.

In the course of a study of the marine organisms causing destruction to submerged timber structures considerable data was accumulated from examination of piles and catamarans and by exposing test panels at selected sites in the harbour and in the open sea, regarding the species of borers active and the intensity of attack of these borers at various sites during the different seasons. Though the series of experiments are being still continued, it was felt that the data collected during 1955 and 1956 may be presented in this paper.

II. *Area surveyed and the timber requirements of the area*

This study was made inside the Madras harbour (Latitude 13 N and 80 E) and the coastal areas north and south of the harbour within the limits of the city and the adjoining rivers Adyar and Cooum.

The Madras harbour is an artificial harbour with an area of 200 acres roughly which is separated from the open sea by built-in concrete break waters. In the main harbour the tide flows rapidly in and out and is subjected to considerable wave action (for fuller details — Refer Daniel 1954). Cross pieces, jetties and piles of west quay, North quay and south quay made

from Pynkado, Oregon Pine, Burma teak, Andaman Paduk, Pyma and Doop and floating fenders and fishing boats made from teak, pine etc. are destroyed by borers.

The main harbour is in communication with a smaller enclosed area of roughly 52,000 sq., ft. called the boat basin where wooden ferry boats of *Lagerstroemia* sp. *Dipterocarpus* sp. and *Tectona* sp. fishing boats, country crafts, jetty piles and floating fenders are in abundance and are destroyed by borers. Hence there is very little exchange of pure water from the open sea as during the tidal inflow only water from the main harbour is forced in, and the water is considerably polluted and impure. The boat basin leads on by a narrow cannal into another enclosed area called the timber pond, where logs of wood are stored.

In the adjoining coastal areas north and south of the harbour within the limits of the city (extending approximately over ten miles) there are more than fifteen fishing Kuppams where approximately three thousand seven-hundred catamarans ** (Each catamaran comprising of three to five logs costing from Rupees seven-hundred to thousand and about fifty masula boats are used by the fisher-folk). From a survey taken at all these fishing Kuppams it was found that these Catamarans are made from (a) *Melia composita,* (b) *Albizzia molluccana,* (c) *Bischofia javanica* and (d) *Erythrina sp.* in the ratio of 8:4:2:1 respectively and that timbers (a) and a part of (b) are imported from Ceylon, the remaining part of (b) being obtained from Malabar, and timbers (c) and (d) being obtained locally. Due to heavy infestation by borers, Catamarans of (a) and (b) have to be replaced every sixth or seventh year and Catamarans (c) and (d) every second or third year. Masula boats made from *Lagerstroemia sp., Dipterocarpus sp.* are also attacked by borers.

The rivers Adyar and Cooum are connected with the sea during the rainy months only and are separated by means of sandbars during summer months. With the onset of the rainy season they become subject to tidal actions. The water is brackish. Fishing crafts and wooden boats carrying various commodities ply in these water ways and are attacked by borers.

**A perusal of the Handbook of Indian Fisheries, 1951, shows that in the Coromandel Coast (i.e.) Pulicat lake to Cape Comorin there are 233 fishing villages where 11,462 catamarans, 1,378 boats and 564 conoes are used by fisherfolk.

TABLE I

Showing data on temperature, Salinity, pH, dissolved oxygen, for the period April 1955 — Dec. '55.

No.	Month	Year		Temperature			pH			Salinity			Oxygen content		
				NNQ	BB	TB	NNQ	BB	TB	NNQ	BB	TB	NNQ	BB	TB
1.	April	1955	..	29·6	29·5	29·6	8·3	8·3	8·4	33·8	33·4	34·0	3·8	3·5	3·85
2.	May	„	..	30	30·3	30	8·4	8·38	8·45	34·3	34·1	34·5	3·9	3·7	3·81
3.	June	„	..	27·2	27·2	27·0	8·3	8·3	8·3	34·0	34·0	34·0	4·0	4·1	4·015
4.	July	„	..	28·1	28·1	28·0	8·3	8·3	8·3	33·6	33·2	33·8	4·0	4·1	3·89
5.	August	„	..	28·2	28·2	28·2	8·3	8·3	8·35	33·9	33·7	34·0	4·1	4·2	3·9
6.	September	„	..	28·2	28·2	28·1	8·3	8·3	8·3	32·4	32·1	33·0	4·1	4·1	3·9
7.	October	„	..	28·2	28·2	28·2	8·2	8·2	8·3	29·9	29·8	30·1	3·98	3·98	3·98
8.	November	„	..	27·0	27·0	27·1	8·2	8·2	8·3	29·9	29·4	30·2	4·1	4·1	4·2
9.	December	„	..	27·1	27·1	27·2	8·3	8·3	8·4	30·0	30·8	30·8	4·2	4·23	4·35

NNQ = New North Quay.
BB = Boat Basin.
TB = Triplicane Beach.

TABLE II

Showing data on temperature, Salinity, pH, and dissolved oxygen, of the surface water at the Madras harbour from January 1956 to December 1956

No.	Month	Year		Temperature	Salinity	pH	Oxygen C. C/L
1.	January	1956	..	26·5	31·5	8·5	4·1
2.	February	„	..	27·5	32·7	8·4	4·2
3.	March	„	..	28·6	33·6	8·5	4·1
4.	April	„	..	29·7	33·9	8·4	4·2
5.	May	„	..	28·9	33·9	8·4	3·9
6.	June	„	..	28·0	34·0	8·3	3·9
7.	July	„	..	27·9	33·8	8·3	4·0
8.	August	„	..	28·1	33·5	8·3	4·0
9.	September	„	..	28·0	33·1	8·2	4·1
10.	October	„	..	28·0	29·9	8·2	4·2
11.	November	„	..	27·5	30·1	8·3	4·1
12.	December	„	..	27·0	31·8	8·4	4·1

III. *Hydrographical data*

Hydrographical data on temperature salinity, pH, and dissolved oxygen, of the surface waters at the main harbour, Boat basin and Triplicane beach from April to December 1955 and in the Main harbour only from January to December 1956 were estimated, every fortnight and averaged for each month. Temperature was recorded by means of a centigrade thermometer. Salinity was determined by Mohr's method of titration of chlorides using silver nitrate. Standard sea water from Copenhagen was used for reference. Hydrogen ion concentration was estimated on the Helligi's comparator using cresol red as indicator. Dissolved oxygen was determined by Winkler's titration method. These data are presented in Tables I & II.

IV. (a) *The Boring Organisms* :—

From the exposed test planks, and from piles, pillars of piers, floating fenders, fishing crafts and masula boats the following organisms were collected from the various sites and are given in Table III.

A total of 18 different species of boring organisms were recorded. Of these only *M. striata, B. carinata, T. manni, T. furcifera, S. terebrans, S. annandalei and Metaponorthus sp.* occurred in appreciable numbers inside the harbour while *M. fragilis, B. carinata, T. diederichsens, T. manni, T. clava and S. terebrans* occurred in abundance in the open sea. In the rivers Adyar and Cooum *M. striata* and *S. terebrans* only occurred.

IV. *The seasonal variations*

To study the concentration of the boring organisms at Madras during various seasons of the year, wooden panels of *Myristica fragrans* measuring 8″ × 10″ × 1″ were immersed one foot below the low tide in the main harbour and opposite to the Triplicane beach in the open sea. These planks were suspended vertically by a pair of stout galvanised copper wires as described in detail in an earlier paper (Daniel, 1954).

Since it was noted that borers affected wood only after the wood was under seawater for two to three months, the panels were conditioned in the laboratory for three months, and immersed one foot below the low tide in the different sites where they were left undisturbed for a month. Periodic and monthly examinations of these planks were made to record the different types of

TABLE III

List of Borers	Main harbour	Boat Basin	Timber Pond	Coastal areas north of harbour	Coastal areas south of harbour	River Adyar	Cooum River
Pholadidae :							
1. *Martesia* (*Martesia*) *striata* Linne ..	P	P	F	F	R	P	F
2. *Martesia* (*Martesia*) *fragilis* Verril and Bush ..	X	X	X	P	P	X	X
Teredinidae :							
3. *Bankia* (*Bankiella*) *carinata* Gray 1827 According to Roch. (Syn. with *B.* (*B*) indica Nair ..	P	P	X	P	P	X	X
4. *Bankia* (*Bankia*) *bipalmulata* Lamark ..	X	X	X	2 spec.	8 spec.	X	X
5. *Bankia* (*Lilobankia*) *campanellata* Moll & Roch 1931 According to Roch. (Syn. with B. (*Bankiella*) *bengalensis* Nair ..	R	X	X	45 spec.	60 spec.	X	X
6. *Bankia* (*Neobankia*) *lineata* Nair 1956 ..	X	X	X	35 spec.	120 spec.	X	X
7. *Bankia* (*Bankiella*) *consularis* Moll 1935 *Syn. B.* (*Bankiella*) *edmondsoni* Nair 1957 ..	X	X	X	2 spec.	4 spec.	X	X
8. *Bankia* (*Neobankia*) *denticuloserrata* Daniel 1957 ..	X	X	X	20 spec.	25 spec.	X	X
9. *Teredo* (*Kuphus*) *manni* (*Wright*) 1866 (*Syn.*) *T. madrasensis* Nair ..	P	P	X	P	P	X	X

10. *Teredo* (*Teredo*) *renschi* Roch 1935 ..	X	X	X	X	35 spec.	X	X
11. *Teredo* (*Teredo*) *furcifera* Martens 1894 According to Roch : Syn. T. (Teredo) parksi Bartsch Syn. T. (Teredo) furcillatus Miller ..	P	P	X	P	P	X	X
12. *Teredo* (*Teredo*) *elongata* Quarf 1849 According to Roch : Syn. with T. navalis of Indian workers ..	R	R	X	R	F	X	X
13. *Teredo* (*Uperotus*) *clava* (Gmelin) .. 1777	R	X	X	R	P	X	X
14. *Teredo* (*Dactylotaredo*) diederichseni Roch 1929 According to Roch : Syn. with T. (Teredora) gregoryii; Dall, Bartsch, Rehder ..	F	X	X	P	P	X	X
Sphaeromidae :							
15. *Sphaeroma terebrans* Bate ..	P	P	X	P	P	P	P
16. *Sphaeroma annandalei* Stebbing ..	P	F	X	X	X	X	X
17. *Sphaeroma walkeri* Stebbing ..	X	F	X	X	X	X	X
18. *Metoponorthus* sp. ..	F	F	X	X	X	X	X

Legend for Table :— P = Plenty (i.e.) 10 or more per test panel of 8″ × 10″ × 1″ for exposure of 30 days.
F = Few (i.e.) 5 to 10 ,, ,, ,, ,, ,, ,, ,, ,, 90 days.
R = Rave (i.e.) 1 to 3 ,, ,, ,, ,, ,, ,, ,, ,, 90 days.
Y = Absent.

* The author is thankful to Dr. Ruth Turner of the Museum of comparative Zoology, Harvard for help in identifying the Pholadidae and to Dr. F. Roch and Dr. G Becker for help in the identification of the Teredinidae.

borers, since, in assessing the actual number of borers, the panels had to be broken open and a fresh set of panels, also preconditioned was substituted every month after examination of the old set of panels. This procedure helped to evaluate the numbers of different active borers in each area during the different months of the year.

The numbers of organisms of *Martesia sp., Bankia sp.* and *Teredo sp.* present on these experimental panels (30 panels in each experiment) were counted and the numbers in a volume of 1 cubic inch was calculated. The data collected were consolidated, averaged and are presented in Tables IV and V.

A perusal of Tables IV and V clearly show that successful settlement and boring of these organisms at tropical Madras occurred right through the year, though marked by seasonal intensity and that these variations are not related to the fluctuations of the hydrographical conditions of the environment. (See tables I & II).

Remarks

How far a test panel with its restricted area can supply data for generalisation regarding boring in waters on large surfaces can be doubtful. However as pointed out earlier by the present author (Daniel 1954) an examination of the experimental panels and adjacent piers and Catamarans for more than three years reveal that all the organisms present in the surrounding area do attach in the experimental plates at some time or other and the data collected are sufficient to draw definite conclusions.

The identity of the main boring organisms in the tropical waters of Madras is now established. In the area studied the main boring organisms are *M. striata, B. carinata T. manni, T. furcifera, S. terebrans, S. annandalei* and *Metaponorthus sp.* inside the Madras harbour while *M. fragilis, B. carinata, T. diederichsens, T. manni, T. clava* and *S. terebrans* are the main borers in the open sea. In the adjacent rivers Adyar and Cooum *S. terebrans* and *M. striata* occur in appreciable numbers.

A comparison of the boring records obtained (see tables IV & V) show that while some species are common to both areas (inside and outside the harbour) there is a difference in the species collected at sites within the harbour and those outside the harbour in the open sea. This difference must be accounted for

TABLE IV

Location site — Madras harbour

Average of 30 panels of size 8″ × 10″ × 1″ in each experiment

No.	Month	Year		Number of organisms per cubic inch: Bankia carinata	Teredo manni	Teredo furcifera	M. striata	Sphaeroma terebrans
1.	April	1955	..	11	4	3	18	18
2.	May	,,	..	9	6	4	15	22
3.	June	,,	..	6	3	2	13	20
4.	July	,,	..	9	4	4	11	22
5.	August	,,	..	10	2	7	18	20
6.	September	,,	..	8	3	7	20	24
7.	October	,,	..	12	5	7	13	18
8.	November	,,	..	13	3	8	16	18
9.	December	,,	..	6	2	6	17	20
10.	January	1956		12	4	6	16	22
11.	February	,,	..	8	3	5	14	20
12.	March	,,	..	10	2	8	12	24
13.	April	,,	..	12	4	6	14	20
14.	May	,,	..	12	4	7	15	18
15.	June	,,	..	11	3	7	14	18
16.	July	,,	..	14	6	6	20	16
17.	August	,,	..	12	2	10	21	20
18.	September	,,	..	10	1	10	16	21
19.	October	,,	..	8	3	11	19	20
20.	November	,,	..	11	2	11	14	19
21.	December	,,	..	8	2	9	14	21

TABLE V

Location site — Open sea (at Triplicane Beach)

Average of 30 panels of size 8″ × 10″ × 1″ in each experiment

No.	Month	Year	Number of Organists per cubic inch									
			Bankia carinata	B. bipalmulata	B. campanallata	Teredo manni	T. diedrenschei	T. clava	T. furcifera	M. striata	M. fragilis	Sphaeroma terebrans
1.	April	1955	16	1	1	4	5	2	1	2	6	14
2.	May	,,	15	2	2	3	4	3	2	2	6	16
3.	June	,,	18	1	2	3	4	3	1	—	8	15
4.	July	,,	20	1	1	2	3	3	1	1	6	18
5.	August	,,	13	1	2	4	4	3	3	2	6	19
6.	September	,,	14	—	2	3	5	4	3	3	11	16
7.	October	,,	20	—	2	3	5	4	4	3	10	18
8.	November	,,	22	—	2	4	4	3	4	2	11	20
9.	December	,,	23	—	1	6	5	4	3	2	12	21
10.	January	1956	16	—	2	5	7	3	—	2	4	20
11.	February	,,	15	—	2	4	4	3	1	2	6	19
12.	March	,,	18	1	1	3	4	2	—	—	8	16
13.	April	,,	17	—	—	3	3	4	1	2	5	18
14.	May	,,	20	—	—	3	4	2	3	2	6	18
15.	June	,,	19	1	—	2	5	1	1	3	10	21
16.	July	,,	20	1	1	5	5	4	—	2	12	22
17.	August	,,	14	1	2	3	4	2	1	2	11	18
18.	September	,,	19	1	2	4	6	3	1	3	10	19
19.	October	,,	22	—	1	4	5	2	—	2	12	17
20.	November	,,	21	—	1	5	4	2	1	3	10	18
21.	December	,,	20	1	1	4	5	2	1	2	11	20

only from the peculiar ecology of the two areas. Within the harbour there is very little exchange of pure water from the open sea as during the tidal inflow only water from the entrance of the harbour is forced in. Moreover, boats are constantly scraped off here and the crushed organisms foul the water. The tidal current is only between 1 to 2·5 knots. In the open sea however this water is fresh and clear but there are heavier water currents. Therefore the animals predominating at different sites are different depending upon the ability of the temporary larval forms to survive in poluted water or otherwise and their settlement in relation to velocity of water currents.

A perusal of tables IV and V showing the attachment of borers right through the year indicate that breeding is continuous. However, in certain months it is more intensified as indicated by increase in the attachment and successful metamorphosis to the adult, in the test panels. It is also seen that variations in the settlement of these borers (Tables IV & V) is not related to the fluctuation of the hydrographical conditions like temperature, salinity, p^h and disolved oxygen of the environment. (See Tables I and II). It is probable that these variations in the settlement of these forms depend on the occurrence of the temporary planktonic larval forms which in turn is related to the reproductive cycle of the adult and availability of food. Apart from these the course of the water currents and wave action is also an important factor in leading the larvae to the particular area where timber is available to ensure successful settlement.

The role played by microorganisms which have to condition wood before further attack by wood borers can take place is a matter which requires further study. The present author while examining experimental panels for fouler and borer attack has found that, in Madras, attack by borers start only after 15 to 20 days of immersion of the panels in sea water and that panels preconditioned in sea water in the laboratory were immediately attacked. Similar observations made in the laboratories at Cuxhaven, Germany lend support to this view. The activities of these microorganisms may help to explain why wood becomes more susceptible to attack as its period of immersion is prolonged.

Summary

The different members of the animal community which bore into timber in the area studied are commented on. The most

important borers are the Pholadids, *Martesia striata* and *Martesia fragilis, the* Teredinids, *Bankia carinata, Teredo manni, Teredo clava, Teredo furcifiera, Teredo diederichsens,* and the isopod, *Sphaeroma terebrans.*

The timber requirements of the area and the destruction caused by these borers at varoius sites are examined. The numbers of different species of borers settling and boring on wooden test panels are recorded from time to time, during the year the experiments were performed and their variations in the different months noted. The presence of microorganisms which have to condition wood before further attack by wood borers can take place is discussed. The difference in the results obtained at different sites are discussed with reference to ecological conditions.

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On the Lattice of Convergence Topologies

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This is an investigation on the structure of certain lattices arising in the theory of convergence topologies on an abstract set. The results relate mainly to the distributive laws satisfied by these lattices, and the nature of the operations of product complementation and sum complementation in them.

INTRODUCTION

The present investigation was carried out during the period (1949-1950) at the instance of Prof. Vaidyanathaswamy; it is a revised and expanded version of the study on the lattice of convergence topologies (on a set R) carried out in his book [4, § 71, p. 267-270].

In the course of this work it was found desirable to consider in addition to the other convergence postulates, two postulates ($\mathbf{P}_4$, $\mathbf{P}_5$) not explicitly mentioned in [4]. These postulates have some lattice-theoretic interest. While Vaidyanathaswamy confined himself mainly to the study of one lattice (the lattice $\mathbf{L}_1$ in our notation) we also investigate the properties of other lattices ($\mathbf{L}_0$, $\mathbf{L}_2$, $\mathbf{L}_3$, $\mathbf{L}_4$) that arise by taking convergence topologies satisfying different combinations of convergence postulates. The different combinations of postulates successively considered constitute axiomatic systems with increasing strength so that in the series of lattices $\mathbf{L}_0 - \mathbf{L}_4$, each is contained in the preceding; further $\mathbf{L}_1$ and $\mathbf{L}_2$ are complete sublattices of $\mathbf{L}_0$. It may be mentioned here that the postulate system corresponding to $\mathbf{L}_0$ is a weakened form of that used by Fréchet to define *L*-spaces, in as much as the requirement for uniqueness of limits has been given up here. Again the postulates corresponding to $\mathbf{L}_1$ form the system proposed by Vaidyanathaswamy [4, p. 267]; and those corresponding to $\mathbf{L}_4$ the system of Urysohn or Kuratowski [3, p. 84].

All the lattices ($\mathbf{L}_0 - \mathbf{L}_4$) are complete. Besides, for the first three lattices ($\mathbf{L}_0 - \mathbf{L}_2$), the lattice operations in each case are just set operations; each lattice is, in fact, dually isomorphic to

a $\Sigma\Delta$-ring of subsets (Rmks. 1, 3). For $\mathbf{L}_3$ and $\mathbf{L}_4$ this is no longer true since lattice product in either case fails to be set product (Thms. 26, 22). Again, while all lattice-sums as well as products are distributive in any of $\mathbf{L}_0$, $\mathbf{L}_1$ and $\mathbf{L}_2$, in $\mathbf{L}_3$ not all infinite lattice sums are distributive (though all infinite products are distributive). (See Thms. 1, 27 & Rmks. 2, 3.) Lastly, $\mathbf{L}_4$ turns out to be a Boolean algebra comprising the common dually normal elements of the lattices $\mathbf{L}_1 - \mathbf{L}_3$ (Thm. 30).

The lattices $\mathbf{L}_0 - \mathbf{L}_2$, it is interesting to observe, are closed for both product and sum complements; $\mathbf{L}_3$, on the other hand, is closed for sum complements alone (see Rmk. 6). Characterizations of the 'product (sum) complement' and the 'normal (dually normal) element' in each of the lattices $\mathbf{L}_0$ and $\mathbf{L}_1$ are obtained in terms of certain properties of 'convergences' belonging to the associated convergence schemes. The introduction of the notions of the 'singular point' and the 'principal (or basic) point' enable elegant characterizations to be given for the product complement' and the 'normal element' (Thms. 5, 6, 15, 16). In the case of $\mathbf{L}_2$ or $\mathbf{L}_3$, the product (sum) complement of an element t coincides with the corresponding product (sum) complement of t in $\mathbf{L}_1$—only, in the case of $\mathbf{L}_3$ the product complement may not always exist (Thm. 28). Further, it is a remarkable fact that the normal elements of $\mathbf{L}_0$ (or $\mathbf{L}_1$) are all simple (Thms. 7, 17).

Finally, some interesting information on the nature of the ordered set $\mathbf{L}_0$ in the vicinity of an element belonging to $\mathbf{L}_1$ is furnished by Theorems 12 and 13.

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1. Preliminaries

Let R be an abstract set (which may be supposed to be infinite to avoid trivialities). Now assume that in R a class t of (infinite) sequences (of not necessarily distinct elements)—called convergent sequences — together with the limit (or limits) of each such sequence is prescribed in some manner so as to satisfy the following basic postulates:

$\mathbf{P}_1$. *If $x \varepsilon R$, the sequence (x_n) with $x_n = x$, for all n, is convergent and converges to the unique limit x.*

P_2. *If the sequence (x_n) is convergent, and converges to a limit x, any subsequence (x_{n_i}) $(n_1 < n_2 < \dots)$ is also convergent, and converges to the same limit x also.*

Any class or scheme t of convergences of the form: $(x_n) \to x$, prescribed in R so as to satisfy $\mathbf{P}_1$ and $\mathbf{P}_2$, is called a C_0-convergence scheme or merely C_0-scheme. The structure induced in R by a C_0-scheme t is called a convergence topology or C_0-topology, and the set R endowed with this structure a limit space (the limit space will be denoted by $(R : t)$).

It is clear from $\mathbf{P}_1$ and $\mathbf{P}_2$ that an arbitrary convergence $(x_n) \to x$ can belong to a C_0-scheme t only if the sequence (x_n) does not contain infinite repetitions of any element $y \neq x$; else by $\mathbf{P}_2$, t would contain a convergence of the form $(x_n) \to x$ with $x_n = y \neq x$ (for all n) contradicting $\mathbf{P}_1$. Any such convergence $(x_n) \to x$ will be called an *admissible* convergence, and the sequence (x_n) will be referred to as an x-admissible sequence.

A convergence $(x_n) \to x$ is called *principal* if $x_n = x$ (for all n); a principal convergence will be denoted in symbols by $(x) \to x$. The totality of principal convergences evidently constitute a C_0-scheme σ_0. Also every C_0-scheme includes all principal convergences. If we call a C_0-topology t_1 'stronger than' a C_0-topology t_2 (in symbols $t_1 \geqslant t_2$) if the set of convergences in the scheme t_1 is a subset of the set of convergences in t_2, then it is clear that '$\geqslant$' partially orders the family $\mathbf{L}_0$ of all C_0-topologies on R. Moreover, it is easy to see that $\mathbf{L}_0$ is a complete lattice, the lattice sum (product) Σt_i (πt_i) of a family of C_0-topologies is the C_0-topology whose convergence scheme is given by the set intersection (union) $\cap [t_i]$ $(\cup [t_i])$ of the sets $[t_i]$ — where $[t_i]$ denotes the set of convergences belonging to t_i. It has σ_0 for its '1' element, and the C_0-topology δ[1] whose convergence scheme comprises all the admissible convergence, as the '0' element.

Remark 1. If $[t]$ denotes as before the set of convergences of the C_0-topology t, then the sets $[t]$ form, as can be easily verified, a $\Sigma\Delta$-ring[2] R_0 of sets. Moreover, the correspondence $t \to [t]$

1. The suffix for δ is dropped as δ is also the '0' element of the lattice $\mathbf{L}_1$ considered latter.

2. I.e., a family of sets closed for arbitrary unions and intersections [4, p. 12].

is a dual (lattice) isomorphism between $\mathbf{L}_0$ and R_0 (lattice sums and products going into set intersections and unions respectively).

2. The Lattice $\mathbf{L}_0$

It follows at once from Remark 1 that

Theorem 1. $\mathbf{L}_0$ *is a completely distributive lattice.*[3]

Corollary. $\mathbf{L}_0$ *is closed for both sum and product complements.*

The corollary results from the well known fact that a complete lattice with all its products (sums) distributive is closed for sum (product) complements.

We next introduce some definitions. If (x_n) is a subsequence of (y_n), (y_n) is called a supersequence of (x_n). An admissible convergence $(y_n) \to x$ is called a superconvergence (subconvergence) of an admissible convergence $(x_n) \to x$, if (y_n) is supersequence (subsequence) of (x_n).

Given a set S of admissible convergences we can generate from it a C_0-scheme $t(S)$ — called the C_0-extension of S by taking the set union of the set S_1 of all subconvergences determined by the convergences in S and the set σ_0 of all principal convergences in R. Evidently $t(S)$ is the strongest C_0-topology under which the convergences in S are valid. From the definition of the C_0-extension we deduce immediately

Theorem 2. *The product completment t' of an element t in* $\mathbf{L}_0$ *is the C_0-extension of the set $c(t)$ of all admissible convergences not belonging to t.*

Alternatively, the product complement can be characterized in terms of superconvergences.

Theorem 3. *A non-principal convergence*[4] $x_n \to x$ *belongs to t', if and only if, it has a superconvergence not belonging to t.*

3. By a completely distributive lattice is meant a complete lattice in which all lattice sums as well as products are distributive; in case of $\mathbf{L}_0$ it is even true (since it is isomorphic with a $\Sigma\Delta$-ring) that the general distributive law [1, p. 146, (22')] holds — this fact is, however, not needed in this paper.

4. Here as well as in the sequel, unless there is explicit mention to the contrary, the mere term 'convergence' is used to mean 'an admissible convergence'.

Proof. By Theorem 2, every non-principal convergence $(x_n) \to x$ belonging to t is a subconvergence of some convergence $(y_n) \to x$ belonging to $c(t)$, and hence not belonging to t. Conversely, if $(x_n) \to x$ has a superconvergence $(y_n) \to x$ not belonging to t, $(y_n) \to x$ must belong to t, since $t.t' = \delta$. Hence by $\mathbf{P}_2$, $(x_n) \to x$ must belong to t. Q.E.D.

The double product complement t'' $(= (t')')$ of a C_0-topology t is specified by

Theorem 4. *A non-principal convergence $(x_n) \to x$ belongs to t'', if and only if, there is a superconvergence $(y_n) \to x$ of $(x_n) \to x$ such that every superconvergence of $(y_n) \to x$ belongs to t.*

Proof. By Theorem 3, a non-principal convergence $(x_n) \to x$ belongs to t'', if and only if, it has a superconvergence $(y_n) \to x$ not belonging to t'; and the last condition holds, if and only if, every superconvergence of $(y_n) \to x$ belongs to t. Q.E.D.

A point x of a C_0-space $(R : t)$ is called a *principal point,* if the only sequence converging to it (under t) is the principal sequence $(x) = (x, x, \ldots)$; otherwise x is called a non-principal point. On the other hand, x is called *a singular point* if every x-admissible sequence in R converges to x; and x is said to be non-singular wherever it fails to be a singular point.

Theorem 5. *If x is a singular point of a C_0-space $(R : t)$, then x is a principal point of $(R : t')$; if x is a non-singular point of $(R : t)$, then x is a singular point of $(R : t')$. Hence every point of $(R : t')$ is either singular or principal.*

Proof. For, if x is a singular point of $(R : t)$ every convergence $(x_n) \to x$ with limit x belongs to $(R : t)$; hence by Theorem 3 no non-principal convergence $(y_n) \to x$ belongs to t', or x is a principal point of $(R : t')$. On the other hand, if x is a non-singular point of $(R : t)$ there exists a non-principal convergence $(y_n) \to x$ not belonging to t. If now $(x_n) \to x$ be an arbitrary (admissible) convergence, then the convergence[5] $(x_n, y_n) \to x$ cannot belong to t by $\mathbf{P}_2$. Hence by Theorem 3, $(x_n) \to x$ belongs to t'. That is, x is a singular point of $(R : t')$. Q.E.D.

5. (x_n, y_n) denotes any sequence (z_n) formed from (x_n) and (y_n) and having (x_n) and (y_n) as subsequences; for example we may set $(x_n, y_n) = (z_n)$ where $z_{2n-1} = x_n$ and $z_{2n} = y_n$.

A C_0-topology t is said to be *normal* if t is a normal element of $\mathbf{L}_0$, i.e., if $t = t''$. The normal C_0-topologies are characterized by

Theorem 6. *A C_0-topology t is normal, if and only if, every non-principal point x of the associated C_0-space $(R : t)$ is singular.*

Proof. First, let t be normal so that $t = (t')'$. Then by applying Theorem 5 twice we obtain that every point of $(R : t)$ is either principal or singular — which proves the 'only if' part.

Next, let t be such that every point of $(R : t)$ is either principal or singular. By Theorem 5 a principal (singular) point x of $(R : t)$ is a singular (principal) point of $(R : t')$, and hence a principal (singular) point of $(R : t'')$. Thus $(R : t) = (R : t'')$ so that $t = t''$, or t is normal. This proves the 'if' part.

Theorem 7. *Every normal element of the lattice $\mathbf{L}_0$ is simple.*[6]

Proof. For, suppose t is a normal element of $\mathbf{L}_0$ and $t + t < o_0$ then some non-principal convergence $(x_n) \to x$ would belong to both t, t'. It follows that x is a non-principal point of $(R : t)$ as well as $(R : t')$. Hence, by Theorem 6, since t, t' are normal elements, x is a singular point of both $(R : t)$ and $(R : t')$. This contradicts Theorem 5, whence $t + t' = o_0$. Q.E.D.

With this we end our discussion of the product complement and pass over to that of the sum complement. The situation here is not quite analogous as will be seen from what follows.

Theorem 8. *A non-principal convergence $(x_n) \to x$ belongs to the sum complement t^*, if and only if, no non-principal subconvergence of $(x_n) \to x$ belongs to t.*

Proof. If $(x_n) \to x$ is a non-principal convergence belonging to t^*, then none of its non-principal subconvergences $(x_{n_i}) \to x$ can belong to t; for else, $(x_{n_i}) \to x$ would be a non-principal convergence common to t, t^*-contradicting the relation $t + t^* = o_0$.

Conversely, if the convergence $(x_n) \to x$ is such that none of its non-principal subconvergences belong to t, then $(x_n) \to x$ must belong to t^*. For otherwise, the convergences belonging to t^* together with all the subconvergences of $(x_n) \to x$ would determine a C_0-topology t_1 with $t + t_1 = o_0$, $t_1 < t^*$; this contradicts the fact that t^* is the sum complement of t. Q.E.D.

6. An element a of a lattice with 0 and 1 is called simple if $a + a' = 1$, $aa' = 0$.

Using the last theorem we can easily show that

Theorem 9. *x is a principal (singular) point of $(R : t^*)$ provided x is a singular (principal) point of $(R : t)$.* (Cf. Thm. 5.)

We shall next prove

Theorem 10. *The double sum complement t^{**} of a C_0-topology t contains a non-principal convergence $(x_n) \to x$, if and only if, t contains a non-principal subconvergence of each of the non-principal sub-convergences of $(x_n) \to x$.*

Proof. Since $t^{**} =$ sum complement of t^*, a non-principal convergence $(x_n) \to x$ belongs to t^{**}, if and only if, no non-principal subconvergence of it belongs to t^* (thm. 8). But the last condition is equivalent to 'every non-principal subconvergence of $(x_n) \to x$ has a non-principal sub-convergence belonging to t'. Q.E.D.

From Theorem 10 we conclude at once that the dually normal C_0-topologies t (i.e., those for which $t^{**} = t$) are precisely those whose convergence schemes satisfy the additional postulate:

P'_6 (Pseudo-normality). *If a non-principal (x-admissable) sequence (x_n) does not converge to x under t, there is a non-principal subsequence of (x_n) none of whose non-principal subsequences converges to x under t.*

3. Other Convergence Postulates

P_3. *A sequence (x_n) converging to a limit x continues to converge to x even after any finite number of terms have been added to it.*

P_4. *A sequence (x_n) converging to x continues to converge to x even after any number of terms each equal to x have been added to it.*

P_5. (Weak-normality). *If a sequence (x_n) is such that it can be split up into two complementary subsequences each converging to x, then (x_n) converges to x.*

P_6. (Normality). *If a sequence (x_n) does not converge to x, then (x_n) has a subsequence none of whose subsequences converges to x.*

The above postulates are not all independent. Their mutual relations as well as their connection with P_1 and P_2 is given by the following scheme where '$\to$' denotes implication

$$(\mathbf{P}_6, \mathbf{P}_2) \begin{array}{l} \nearrow \mathbf{P}_3 \\ \searrow \mathbf{P}_5 \end{array} \quad : (\mathbf{P}_5, \mathbf{P}_1) \rightarrow \mathbf{P}_4$$

Thus for a C_0-topology we have (A) $\mathbf{P}_6 \rightarrow \mathbf{P}_5 \rightarrow \mathbf{P}_4$; $\mathbf{P}_6 \rightarrow \mathbf{P}_3$.

The following theorem is an immediate consequence of the definition of the lattice sum Σt_i (product πt_i) of a family of C_0-topologies t_i.

Theorem 11. *The C_0-topology Σt_i will satisfy* $\mathbf{P}_j$ $(j = 3, 4, 5,$ or $6)$ *provided each t_i satisfies* $\mathbf{P}_j$. *The C_0-topology πt_i will satisfy* $\mathbf{P}_j$ $(j = 3$ *or* $4)$ *provided each t_i satisfies* $\mathbf{P}_j$.

We shall call a C_0-topology satisfying $\mathbf{P}_3$ a C_1-topology, and a C_1-topology satisfying $\mathbf{P}_j$ $(j = 4, 5$ or $6)$ a C_{1j}-topology. In view of the implications (A), a C_{16}-topology is a C_{15}-topology, and a C_{15}-topology, a C_{14}-topology. On the other hand, the following examples show that a C_{15}-topology need not be a C_{16}-topology, and that a C_{14}-topology need not be a C_{15}-topology.

Example 1. R is the set of non-negative integers. A C_0-topology t is defined by the requirement: a convergence $(x_n) \rightarrow x$ belongs to t, if and only if, either (i) $(x_n) \rightarrow x$ is basic (see definition below), or (ii) $x = 0$, and all the $x_n \neq 0$ constitute a finite or rapidlly divergent set. (A set (a_n) of positive integers is called rapidly divergent if $\alpha(N)/N \rightarrow 0$, as $N \rightarrow \infty$, where $\alpha(N)$ denotes the number of a_n's $\leqslant N$).

It is clear that t satisfies $\mathbf{P}_1$ and $\mathbf{P}_3$. Since a subset of a rapidly divergent subset is either finite or rapidly divergent, t satisfies $\mathbf{P}_2$. Further, since the union of two rapidly divergent subsets is also rapidly divergent [4, p. 26, Ex. 20] t satisfies $\mathbf{P}_5$. Finally, it does not satisfy $\mathbf{P}_6$. For, consider the convergence $(n) = (1, 2, \ldots) \rightarrow 0$ which does not belong to t (since the set (n) is not rapidly divergent). Every subsequence of (n) contains a subsequence converging to 0 under t. This is because every infinite set $A = (a_n)$ of (distinct) positive integers contains a rapidly divergent subset (sufficient to choose $a_n > n^2$ which is possible since there are only a finite number of a_n's $\leqslant n^2$). Thus t is a C_{15}-topology but not C_{16}-topology.

Example 2. The following definition of convergence in real number space R obviously gives rise to a C_{14}-topology t which is not a C_{15}. A sequence (a_n) in R converges to a (under t) if it con-

verges to a in the usual sense and further there exists an integer N such that for $n \geqslant N$, either (1) $a_n \leqslant$ or (2) $a_n \geqslant a$.

The bearing of $\mathbf{P}_3$ on the partial ordering relation in $\mathbf{L}_0$ is brought out by the following propositions.

Theorem 12. *Given a C_1-topology t_1 and a C_0-topology t_0 with $t_1 < t_0$, there exists a C_0-topology t_0^1 with $t_1 < t_0^1 < t_0$.*

Proof. For, by hypothesis, we can find a convergence (c_1): $(x_n) \rightarrow x$ (which must be non-principal) belonging to t_1 but not to t_0. Let x_k be the first element in the sequence (x_n) different from x. Since there can only be a finite number of repetitions of x_k in (x_n), there exists an integer N such that $x_n \neq x_k$ for $n > N$.

Now choose elements y, z in R (which we have assumed to be infinite) with $y \neq z$; $y \neq x_r$ $(r=1, 2, \ldots N)$; $z \neq x$, x_r $(r=1, 2 \ldots N)$. Adjoin the subconvergences of (c_2): $(y, (x_n)) = (y, x_1, x_2, \ldots) \rightarrow x$, to t_0 and thereby obtain a C_0-topology t_0^1. Then clearly $t_0^1 < t_0$ (since (c_1) belongs to t_0^1 but not to t_0).

The convergence (c_3): $(z, y, (x_n)) \rightarrow x$ belongs to t_1 (by $\mathbf{P}_3$). However, (c_3) does not belong to t_0^1. For in the first place, (c_3) as a superconvergence of (c_1)—which itself does not belong to t_0—cannot belong to t_0. Next, by our choice of z, (c_3) can never be a subconvergence of (c_2). (For then we would have a $z = x_p$, $x_k = x_q$, for some p, q with $q > p > N$—an impossibility). Hence, from the definition of t_0, (c_3) cannot belong to t_0^1. Thus $t_1 < t_0^1$, completing the proof.

Note that we could not have assumed y, z, $\neq x_n$ (for all n)—and thereby simplified the argument—since R need not necessarily be uncountable.

Theorem 13. *If t_1 be a C_1-topology and t_0 a C_0-topology such that $t_0 < t_1$, there exists a C_0-topology t_0^1 with $t_0 < t_0^1 < t_1$.*

Proof. Since $t_0 < t_1$, there exists a (non-basic) convergence (c_1): $(x_n) \rightarrow x$ belonging to t_0 but not to t_1. Let x_k be the first term of the sequence (x_n) different from x, and N be an integer such that $x_n \neq x_k$ for $n > N$. Then convergence (c_2): $(y_n) \rightarrow x$—where (y_n) is a sequence resulting from (x_n) by deleting its first N terms—does not belong to t_1 (since otherwise by $\mathbf{P}_3$, (c_1) would also beong to t_1). It follows that by adjoining the subconvergences of (c_2) to t_1 we obtain a C_0-topology t_0^1 with $t_0^1 < t_1$. Again

since (c_1) is not a subconvergence of (c_2) because $x_k \varepsilon (x_n), x_k \varepsilon (y_n)$, ($c_1$) cannot belong to t_0^1 and hence $t_0 < t_0^1$.

Remark. Theorems 12 and 13 show at once that a C_1-topology t cannot be an upper or a lower jump element[7] of $\mathbf{L}_0$. Hence the two sections $\{(K_1, t), K_2\}$, $\{K_2, (t, K_2)\}$ determined by t—where K_1, K_2 are the sets of elements of $\mathbf{L}_0$ which are 'less than' and 'greater than' t respectively—are both cuts.[7]

We close this section with some definitions relating to sequences and convergences which will be required in the sequel.

Definition. A sequence (x_n) is called *basic* if there exists an integer n such that $x_n = x_{n+1} = x_{n+2} = \ldots$; $(x_n) \to x$ is said to be a *basic convergence* if $x_n = x_{n+1} = x_{n+2} = \ldots. = x$. A basic sequence (x_n) if convergent under a C_0-topology t must (by $\mathbf{P}_1$ & $\mathbf{P}_2$) necessarily converge to the *unique* limit $x (= x_n = x_{n+1} = \ldots)$ already determined by the sequence itself (and so independent of t). Given a C_1-topology t and a point $x \varepsilon R$, x is called a basic *point* of the limit space $(R : t)$ if every sequence converging to x under t is basic.

A sequence (x_n) is called *regular* if it contains infinite repetitions of no element; $(x_n) \to x$ is called a *regular convergence* if the sequence (x_n) is regular. If a point $x \varepsilon R$ is such that all regular sequences (in R) converge to it under t then x is called a *regular point* of $(R : t)$.

4. THE LATTICE $\mathbf{L}_1$

The totality σ of basic convergences in R evidently defines the strongest c_1-topology on R. On the other hand, the set δ of all (admissible) convergences in R satisfies $\mathbf{P}_3$ (in addition to $\mathbf{P}_1$ and $\mathbf{P}_2$), and hence defines the weakest C_1-topology on R. These facts together with Theorem 11 imply at once:

Theorem 14. *The set $\mathbf{L}_1$ of all C_1 topologies on R is a complete sublattice of the lattice*[8] *$\mathbf{L}_0$ (of all C_0-topologies on R) whose lower unit δ is the same as that of $\mathbf{L}_0$; the upper unit σ is the C_1-topology comprising the basic convergences in R.*

7. For definitions, vide [4, p. 38].

8. I.e., $\mathbf{L}_1$ is a complete lattice, and an arbitrary lattice sum (product) in $\mathbf{L}_1$ coincides with the corresponding sum (product) in $\mathbf{L}_0$.

Remark 2. Since $\mathbf{L}_1$ is a complete sublattice of the completely distributive lattice (see footnote 1) $\mathbf{L}_0$, it follows that L_1 itself is completely distributive, and hence closed for both product complements and sum complements.

The next few theorems (Thms. 15-19) relating to 'product complement', 'sum complement', and 'normal element' in $\mathbf{L}_1$ are exact analogues of the corresponding results for $\mathbf{L}_0$. The proofs are all omitted since they are just repetitions of those given for the counterparts (for $\mathbf{L}_0$).

Theorem 15. *If x is a singular point of $(R : t)$, then x is a basic point of $(R : t')$; if x is a non-singular point of $(R : t)$, then x is a singular point of $(R : t')$. Hence every point of $(R : t')$ is either singular or basic.*[9] (Cf. Thm. 5.)

(Here t is an element of L_1 and t′ its product complement in L_1).

Theorem 16. *A C_1-topology t is normal (i.e., is a normal element of $\mathbf{L}_1$), if and only if, every non-basic point of $(R : t)$ is singular.* (Cf. Thm. 6.)

Theorem 17. *Every normal element of L_1 is simple.* (Cf. Thm. 7.)

Theorem 18. *A non-basic convergence $(x_n) \rightarrow$ x belongs to the sum complement (in $\mathbf{L}_1$) t^* of a C_1-topology t, if and only if,*

(A): no non-basic subconvergence of $(x_n) \rightarrow x$ belongs to t[10]. (Cf. Thm. 8.)

Corollary. *A basic (regular) point of $(R : t)$ becomes a singular (basic) point of $(R : t^*)$.*

Proof. If x is a basic point of $(R : t)$, then evidently every non-basic convergence $(x_n) \rightarrow x$ (with x as limit) satisfies condition (A) of the theorem and hence belongs to t^*; that is, x is a singular point of $(R : t^*)$. On the other hand, if x is a regular

9. This is the correct form of the result erroneously stated in [4, § 71.2].

10. The specification of t^* as given in [4; § 71.3] is incomplete since it is based on the false conclusion stated therein that all convergences of a C_1- called there as L-) topology are determined once all regular convergences belonging to it are known (this is true only of a C_u-topology).

point of $(R:t)$, no non-basic convergence $(x_n) \to x$ belongs to t^* since every such convergence obviously contains a regular subconvergence which belongs to t because x is regular; this means that x is a basic point of $(R:t^*)$. Q.E.D.

Remark. Note that the latter part of the above result is slightly stronger than its analogue contained in Theorem 9, in as much as it is shown here that any regular (and not necessarily singular) point of $(R:t)$ becomes a basic point of $(R:t^*)$.

Theorem 19. *A non-basic convergence $(x_n) \to x$ belongs to the double sum complement (in $\mathbf{L}_1$) t^{**} of a C_1-topology t, if and only if, t contains a non-basic subconvergence of each non-basic subconvergence of $(x_n) \to x$.* (Cf. Thm. 10.)

Corollary. *A regular convergence $(x_n) \to x$ belongs to t^{**} if and only if, t contains a subconvergence of every subconvergence of $(x_n) \to x$.*

(This follows from the theorem by observing that every subconvergence of a regular convergence is non-basic).

We now show that the result contained in the previous corollary is true not only for a regular convergence but also for an arbitrary convergence (whether admissible or not) so that we have

Theorem 20. *The double sum complement t^{**} of a C_1-topology t contains an arbitrary convergence (c_1): $(x_p) \to x$, if and only if,*

(B) every subconvergence of (c_1) has a subconvergence belonging to t.[11]

Proof. First, let the convergence (c_1) satisfy the condition (B). Then (c_1) must necessarily be *admissible.* For else, (c_1) would contain a subconvergence of the form (c_1'): $(y) = (y, y, \ldots) \to x$ $(y \neq x)$, and clearly t cannot contain any subconvergence of (c_1') contradicting (B).

Since t^{**} — as a C_1-topology — contains all basic convergences, we may assume that (c_1) is non-basic. Let (c_2) denote any non-basic subconvergence of (c_1). Then clearly (c_2) has a regular subconvergence (c_3). By condition (B), there is a subconver-

11. This proposition has been correctly stated in [4, § 71.3, p. 269]. But the proof given there is incomplete for the reason stated in footnote 10.

gence (c_4) of (c_3) belonging to t: also (c_4) is a non-basic subconvergence (since (c_3) is regular). Hence, (c_2) has as one of its subconvergences the non-basic convergence (c_4) belonging to t. It follows by Theorem 19 that (c_1) belongs to t^{**}. This proves the sufficiency of the condition B.

Next, to prove the necessity of (B), assume that (c_1): $(x_n) \to x$ belongs to t^{**} and that (c_2) is any subconvergence of (c_1). We may clearly assume further that (c_1) and (c_2) are non-basic. Then (c_2) has a regular subconvergence (c_3)—which as a subconvergence of (c_1) belongs to t^{**}. By Corollary to Theorem 19, (c_3) has a subconvergence (c_4) belonging to t. Since (c_4) is also a subconvergence of (c_2), condition (B) holds—which completes the proof.

The last theorem states: a sequence (x_n) converges to x under t^{**}, if and only if, every subsequence of (x_n) has a subsequence converging to x under t. Since $t^{**} \leqslant t$, it follows that convergence schemes for which $t = t^{**}$ are precisely those that satisfy the condition.

(D) A sequence (x_n) converges to x under (under t) if and only if, every subsequence of (x_n) has a subsequence converging to x (under t).

This condition (D) is clearly equivalent to the postulate $\mathbf{P}_6$. Thus we obtain

Theorem 21. *The C_{16}-topologies are precisely the dually normal elements $t\,(t = t^{**})$ of the lattice $\mathbf{L}_1$.*

Using known results[12] in Lattice theory we conclude from the previous theorem:

Theorem 22. *The family of C_{16}-topologies constitute a complete Boolean algebra $\mathbf{L}_4$ which is a completely additive system of $\mathbf{L}_1$, and has the same units (δ, σ) as $\mathbf{L}_1$. If (Σ_4, π_4), (Σ_1, π_1) dentoe the lattice operations in $\mathbf{L}_4$ and $\mathbf{L}_1$, then (t_i being any family of elements of $\mathbf{L}_4$)*

$$\Sigma_4 (t_i) = \Sigma_1 (t_i)$$

$$\pi_4 (t_i) = t^{**} \text{ where } t = \pi_1 (t_i).$$

12. The dually normal elements of any complete distributive lattice $\mathbf{L}_1$, closed for sum complements form a Boolean algebra $\mathbf{L}_4$ which is a completely additive system of $\mathbf{L}_1$; the lattice operations in $\mathbf{L}_1$ and $\mathbf{L}_4$ are related as stated in Thm. 22 (cf. [4, p. 45, ex. 12]).

An interesting property of the Boolean algebra $\mathbf{L}_4$ is afforded by

Theorem 23. *The Boolean algebra* $\mathbf{L}_4$ *(of C_{16}-topologies) has no minimals*[13] *and (consequently) also no maximals.*[13]

Proof. For, if $t \varepsilon \mathbf{L}_4$ and $t \neq o$, there exists an admissible convergence (c_1): $(x_n) \rightarrow x$ not belonging to t. By Theorem 20 we can find a subconvergence $(y_n) \rightarrow x$ (of (c_1)) such that none of its subconvergences belong to t. It follows that (y_n) is a regular sequence; let (y_n) be split up into two complementary subsequences $(y_{n'})$ and $(y_{n''})$. Now construct a new C_{16}-topology t_1 as follows: every point of $(R : t_1)$ except x shall be singular; an x-admissible sequence (z_n) shall converge to x, if and only if, (z_n) contains at most a finite number of $y_{n'}$'s. By this requirement $\mathbf{P}_6$ is not violated since $(y_{n'})$ being regular contains utmost a finite number of terms each equal to x; again it is obvious that $\mathbf{P}_1$ and $\mathbf{P}_2$ are also not violated.

Next, let an x-admissible sequence (z_n) not converge to x under t_1; then (z_n) contains a subsequence of the $y_{n'}$'s — which does not converge to x under t (by our hypothesis on (y_n)). Hence (z_n) cannot converge to x under t. This proves $t_1 \leqslant t$. Finally, $t_1 \neq t$ since $(y_{n''}) \rightarrow x$ belongs to t_1 but not to t. Thus, if $t \neq o$, we can find a t, with $t_1 < t$. This means that $\mathbf{L}_4$ has no minimals.

Remark. Since $\mathbf{L}_4$ has no minimals it cannot satisfy (by Tarski's well known result) the complete distributive law of set algebra, and hence it cannot be dually isomorphic to a $\Sigma\Delta$-ring of sets (cf. Rmk. 1).

5. THE LATTICES $\mathbf{L}_2$ AND $\mathbf{L}_3$

It follows at once from their definition that the C_1-topologies (δ, o) (the units of $\mathbf{L}_1$) satisfy the postulate $\mathbf{P}_5$ and hence also $\mathbf{P}_4$. Furthermore, we conclude immediately from Theorem 11:

Theorem 24. *The totality of C_{14}-topologies on a set R is a complete sublattice* $\mathbf{L}_2$ *of each of the complete lattices* $\mathbf{L}_0$, $\mathbf{L}_1$; *the units of* $\mathbf{L}_2$ *are the same as those of* $\mathbf{L}_1$.

13. An element a of a destributive lattice L with 0 and 1 is called a minimal if $a \neq 0$ and $b < a$ implies $b=0$; dually a maximal is defined.

Remark 3. Since $\mathbf{L}_2$ and $\mathbf{L}_1$ (see Thm. 14) are each a complete sublattice of $\mathbf{L}_0$, and $\mathbf{L}_0$ is dually isomorphic to a $\Sigma\Delta$-ring of sets (Rmk. 1) it is clear that each of $\mathbf{L}_2$ and $\mathbf{L}_1$ is also dually isomorphic to a $\Sigma\Delta$-ring of sets.

Theorem 25. *The totality of C_{15}-topologies on R is a complete lattice $\mathbf{L}_3$; $\mathbf{L}_3$ is a completely additive subsystem of each of the lattices $\mathbf{L}_0$, $\mathbf{L}_1$, $\mathbf{L}_2$. The units of $\mathbf{L}_3$ are identical with those of $\mathbf{L}_1$ (or $\mathbf{L}_2$).*

Remark 4. The lattices $\mathbf{L}_i$ $(i=0, 1, 2, 3, 4)$ are connected by the relation of (strict) set inclusion thus: $\mathbf{L}_4 \subset \mathbf{L}_3 \subset \mathbf{L}_2 \subset \mathbf{L}_1 \subset \mathbf{L}_0$.

Next we prove:

Theorem 26. *The lattice product $\pi^* t_a$ of a family (t_a) of elements of $\mathbf{L}_3$ is specified by the convergence scheme: a convergence (c_1): $(x_n) \to x$ belongs to $\pi^* t_a$, if and only if, either (i) the convergence (c_1) belongs to some t_a or (ii) the sequence (x_n) can be decomposed into a finite number of disjoint subsequences s_j such that the convergence $s_j \to x$ belongs to t_j $(j=1, 2, \ldots\ldots m)$.*

Proof. For, if t_0 denote the convergence topology defined by the above scheme, it is clear that t_0 satisfied $\mathbf{P}_1$, $\mathbf{P}_2$, $\mathbf{P}_3$ and $\mathbf{P}_5$ (so that $t \in \mathbf{L}_3$); and also that $t_0 \leqslant$ (each) t_a. To complete the proof we have to show that, if t be any element in $\mathbf{L}_3$ and $t \leqslant t_a$ then $t \leqslant t_0$. If (c_1): $(x_n) \to x$ belongs to t_0 but not to any t_a then $s=(x_n)$ admits a decomposition into a finite number of disjoint sequences s_j $(j=1, 2, \ldots, m)$ such that the convergence $s_j \to x$ belongs to t_j. Since $t \leqslant t_j$, the convergence $s_j \to x$ belongs to t, and hence by $\mathbf{P}_5$, the convergence (c_1) also belongs to t. On the other hand, if (c_1) belongs to t_0 *and* also to some t_a—say $t_{a'}$, then (c_1) belongs to t since $t \leqslant t_{a'}$. Thus, $t \leqslant t_0$, as was required to be shown.

Remark 5. Since lattice product differs from (the corresponding) set product, $\mathbf{L}_3$ is not dually isomorphic to any $\Sigma\Delta$-ring of sets.

Theorem 27. *The complete lattice $\mathbf{L}_3$ has all its products (and therefore also finite sums) distributive; but not all infinite sums are distributive in $\mathbf{L}_3$.*

Proof. To prove the first part, it is sufficient (by virtue of one-sided distributive law) to show that (i) $t + \pi^* t_a \geqslant \pi^* (t + t_a)$. Now, any convergence (c_1): $(x_n) \to x$ belonging to $(t + \pi^* t_a)$ must belong to t as well as to $\pi^* t_a$. From Theorem 26 it follows that either (c_1) belongs to some $t_a = t_{a'}$ in which case it also belongs to $\pi^* (t + t_a)$ (since $\pi^* (t + t_a) \leqslant t + t_{a'}$ and (c_1) belongs to $t_{a'}$); or the sequence (x_n) admits a decomposition into a finite number of subsequences s_j with $s_j \to x$ belonging to t_j $(j = 1, 2, \ldots, m)$. By $\mathbf{P}_2$ each $s_j \to x$ also belongs to t. Hence $s_j \to x$ belongs to $t + t_j$, and consequently *all* $s_j \to x$ belong to $\pi^* (t + t_a)$. Therefore by $\mathbf{P}_5$, (c_1) also belongs to $\pi^* (t + t_a)$, which completes the proof of the inequality (i).

For proving the second part, let R be decomposed as $R = X + Y + Z$, where $X = (x)$ is a one element set, $Y = (x_{ij})$ a set consisting of an infinite double array of elements x_{ij} and $Z = R - (X + Y)$.

Now define a family of C_{14}-topologies: $(t, t_i \ (i = 1, 2, \ldots.))$ on R as follows:

t: all points of $(R : t)$ except x are to be taken as basic; a non-basic convergence $(x_n) \to x$ $(x_n \varepsilon R)$ shall belong to t, if and only if, the sequence (x_n) does not contain terms from more than a finite number of distinct rows of Y.

t_i: all points of $(R : t_i)$ except x to be basic; a non-basic convergence $(x_n) \to x$ shall belong to t_i, if and only if, (x_n) contains utmost a finite number of terms from the i-th row of Y.

It is easy to verify that t, t_i satisfy all the postulates for a C_{14}-topology. We will now show that $t \times (\Sigma t_i) \neq (t \times t_i)$ (where Σ, $\times$ denote lattice operations in $\mathbf{L}_3$) by exhibiting a convergence $s \to x$ belonging to the R.H.S. of this inequality but not to its L.H.S. Let (x_{ij}) be rewritten as a sequence $s = (x_n)$. Let s_i denote the subsequence of s comprising all terms of (x_{ij}) except those occurring in the i-th row, and s_i^* that consisting of terms of the i-th row. Then $s_i \to x$ belongs to t_i, and $s^* \to x$ to t. Therefore, by Theorem 26, $s \to x$ belongs to (each) $t \times t_i$ and hence also to $\Sigma (t \times t_i)$. But $s \to x$ does not belong to $t \times (\Sigma t_i)$.

For, were that true then s could be decomposed into complementary sequences s_0, s_0^* such that $s_0 \to x$ belongs to t, and $s_0^* \to x$ to Σt_i. It follows from the definition of t that an i_0-th row of the

array can be found which is disjoint with s_0. Hence all terms of this i_0-th row belong to s_0^* so that $s_0^* \rightarrow x$ does not belong to t_{i_0}. But this contradicts the relation to $t_{i_0} \leqslant \Sigma t_i$. Q.E.D.

Remark 6. Since the $\mathbf{L}_1$ — sum complement (*i.e.* sumcomplement in $\mathbf{L}_1$) t^* of a C_1-topology t is a dually normal element of $\mathbf{L}_1$, it follows that t satisfies $\mathbf{P}_6$ (Thm. 21) and hence also $\mathbf{P}_5$ and $\mathbf{P}_4$. Hence since $\mathbf{L}_2$, $\mathbf{L}_3 \subset \mathbf{L}_1$, it results that that the $\mathbf{L}_2$ — ($\mathbf{L}_3$ —) sum complement of an element in $\mathbf{L}_2$ ($\mathbf{L}_3$) — which exists since $\mathbf{L}_2$ ($\mathbf{L}_3$) is complete and has all products distributive (Thms. 24, 27) — coincides with the $\mathbf{L}_1$ — sum complement of the same element. In a similar manner, using Theorem 15, we can show that the $\mathbf{L}_2$ — product complement of an element of $\mathbf{L}_2$ is the same as its $\mathbf{L}_1$—product complement. But with regard to $\mathbf{L}_3$ — product complement of an element of $\mathbf{L}_3$, we can only state : whenever the $\mathbf{L}_3$ — product complement exists, it coincides with the corresponding $\mathbf{L}_1$ — product complement. The reason for this modification is that unlike $\mathbf{L}_2$, $\mathbf{L}_3$ need not be closed for product complements. Collecting these results together we obtain

Theorem 28. *The Lattices $\mathbf{L}_2$ and $\mathbf{L}_3$ are both closed for sum complements, the sum complement of an element t in $\mathbf{L}_2$ or $\mathbf{L}_3$ coinciding with that of t in $\mathbf{L}_1$. The lattice $\mathbf{L}_2$ is also closed for product complements, the product complement of an element in $\mathbf{L}_2$ being the same as its product complement in $\mathbf{L}_1$. Finally, whenever the product complement (in $\mathbf{L}_3$) of an element in $\mathbf{L}_3$ exists, it is identical with the corresponding product complement in $\mathbf{L}_1$ (or $\mathbf{L}_2$) — which always exists.*

Theorem 29. *If t is a simple element of $\mathbf{L}_1$, then t' (product complement of t in $\mathbf{L}_3$) exists, and t (and therefore also t') is a simple element of $\mathbf{L}_3$.*

Proof. If t^* denote sum complement of t in $\mathbf{L}_1$ and therefore also in $\mathbf{L}_3$ (Thm. 28), then $t + t^* = \sigma$, $t \,.\, t^* = \delta$ (since t is simple; (.) denotes product in $\mathbf{L}_1$). Further since $\mathbf{L}_3 \subset \mathbf{L}_1$ we have $t \times t^* \leqslant t.t^* = \delta$ (($\times$) denoting product in $\mathbf{L}_3$), *i.e.*, $t \times t^* = \sigma$. Thus, $t + t^* = \sigma$, $t \times t^* = \delta$ and hence t, and also $t' = t^*$, are simple.

Remark. The converse of the above theorem is not true — that is, a simple element of $\mathbf{L}_3$ could fail to be a simple element of $\mathbf{L}_1$. For, consider the simple element t of $\mathbf{L}_3$ defined as follows.

First, let R be decomposed in some way into disjoint sets, as $R = (x) + Y + Z$ where x is a point of R, Y and Z some suitable infinite sets. Next, all points of $(R : t)$ except x are taken as basic. Further, a non-basic convergence $(x_n) \rightarrow x$ is required to belong to t, if and only if, (x_n) contains at most a finite number of elements from Z. Then, if t^* denote sum complement of t in $\mathbf{L}_1$ (or $\mathbf{L}_3$), $(R : t^*)$ has all points except x singular (Thm. 18, Cor.). Also, a convergence $(x_n) \rightarrow x$ belongs to t^*, if and only if, (x_n) contains at most a finite number of elements from Y. Hence, it follows from Theorem 26 that $t \times t^* = \delta$ — so that t is a simple element of $\mathbf{L}_3$. On the other hand, $t.t^* \neq \delta$ since a convergence $(x_n) \rightarrow x$ — with the sequence (x_n) containing an *infinity* of elements from *each* of Y, Z — does not belong to $t.t^*$. Hence t is not a simple element of $\mathbf{L}_1$ (however, t is a dually normal element of $\mathbf{L}_1$ in view of Thm. 30).

Finally, we conclude with

Theorem 30. *Each of the lattices* $\mathbf{L}_1$, $\mathbf{L}_2$, $\mathbf{L}_3$ *has for its Boolean algebra of dually normal elements, the same set* $\mathbf{L}_4$ *comprising of all the* C_{16}*-topologies (on* R*).*

Proof. This follows from the relation $\mathbf{L}_1 \supset \mathbf{L}_3 \supset \mathbf{L}_2 \supset \mathbf{L}_4$ (Rmk. 4), the fact that the sum complementation in $\mathbf{L}_2$ or $\mathbf{L}_3$ coincides with that in $\mathbf{L}_1$ (Thm. 28), and Theorem 22.

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Ternary Systems with Ethylene Glycol

BY

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ABSTRACT

Solubility data and equilibrium phase compositions were measured at 30°C for the following ternary liquid systems:—ethylene glycol-water-methyl acetate, ethylene glycol-water-ethyl formate, ethylene glycol-water-cyclohexanon and ethylene glycol-water-Methylisobutylketone. The equilibrium results indicate that the ratio of the glycol concentration in water to that in the above solvents is greater than unity as in the case of alcohols, furfural and methyl ethyl ketone previously studied as solvents for the extraction of glycol from aqueous solutions. The tie line data have been correlated by the methods of Bachman, Hands and Othmer and Tobias.

Introduction

Potentialities of liquid-liquid extraction technique as a means of separating liquid components from their solutions when other vapourisation methods are impractical or costly, have been increasingly recognised in recent years and need has been felt for reliable liquid equilibrium data. Considerable interest has been shown for the extraction of glycol from aqueous solution by means of liquid-liquid extraction technique. Laddha and Smith (1948) investigated the extraction of glycol from aqueous solution and considered n-amyl alcohol and n-hexyl alcohol as solvents. Conway and Norton (1951) studied the system ethylene glycol — furfural — water. Lakshminarasimhan, Gopalan and Laddha (1956) evaluated the performance of n-butyl alcohol and isobutyl alcohol as extraction solvents. Raja Rao and Venkata Rao (1957) have given ternary equilibrium data for the ternary systems with n-butanol and methyl ethyl ketone at 27°C and 30°C respectively. A further study indicated that methyl acetate, ethyl formate, cyclohexanon and methyl isobutyl ketone could be used as solvents. The present investigation was undertaken to determine the complete mutual solubility and phase distribution data for the following systems at 30°C.

1. Ethylene glycol — Water — Methyl acetate.
2. Ethylene glycol — Water — Ethyl formate.
3. Ethylene glycol — Water — Cyclohexanon.
4. Ethylene glycol — Water — Methyl isobutyl ketone.

Experimental

Materials Used:

1. Ethylene glycol:—Ethylene glycol was purified by vacuum distillation. It had a density of 1·1064 at 30°C.

2. Methyl acetate:—Methyl acetate supplied by E. Merck Darmstadt was fractionated and the fraction boiling between 56·5 — 57·2 was used. It had a density of 0·9228 at 30°C.

3. Ethyl formate:—Laboratory reagent grade Ethyl formate supplied by British Drug Houses was fractionated and the fraction boiling at 54·2°C was used. It had a density of 0·9100 at 30°C.

4. *Cyclohexanon*:—Cyclohexanon supplied by Thomas Tyrer and Company Ltd., London was distilled and the fraction distilling at 155·5°C was used. It had a density of 0·9378 at 30°C.

5. Methyl isobutyl ketone:—Laboratory reagent grade methyl isobutyl ketone supplied by British Drug Houses was fractionated and the fraction boiling at 116°C was used. It had a density of 0·7922 at 30°C.

6. Distilled water from the Laboratory supply was used.

Experimental Procedure:

Determination of the limiting solubility and the tie lines in the ternary systems at 30°C were made by the method described by Othmer et al (1941, 1942). Mixture of glycol and water, or glycol and solvent of known concentration were held in a water bath at 30° ± 0·1°C and were titrated with the third component until the appearance of turbidity indicating the limiting solubility concentration. To determine the tie lines, known mixtures of such compositions within the two phase region were prepared and agitated in the water bath for a minimum period of 4 hours. When the two separated phases were clear, the individual phases were separated and weighed. The composition of each phase was evaluated by the solution of the necessary material balance relations taking advantage of the fact that these must lie on the equilibrium curve. The extremeities of the tie lines thus determined were also checked by determining the density of each layer and by determining the glycol content of each layer volumetrically by the method suggested by Curme and Johnston (1952).

Results and Correlations:

The solubility and tie line data for the four ternary systems are summarised in Tables I, II, III and IV. The binodal curves for the ternary systems are plotted in Figures 1, 2, 3 and 4.

Table 1

Equilibrium Data for the System Ethylene Glycol — Methyl Acetate — Water at 30°C.

Solubility Data			Weight Percentage		
Clycol	Methyl Acetate	Water	Glycol	Methyl Acetate.	Water
—	25·47	74·53	—	90·65	9·35
14·62	25·19	60·19	4·38	89·20	6·42
30·00	26·29	43·71	6·50	87·81	5·69
37·28	27·83	34·89	9·48	86·32	4·20
44·16	30·87	24·97	11·20	84·78	4·02
48·52	34·45	17·03	20·63	76·03	3·34
50·19	41·41	8·40	35·00	61·80	3·20
46·46	48·60	4·94	—	—	—

TIE LINE DATA

Ester Phase Composition Wt. %			Water Phase Composition Wt. %		
Glycol	Methyl Acetate.	Water	Clycol	Methyl Acetate	Water
1·42	90·10	8·48	12·64	25·16	62·20
3·25	89·60	7·15	22·24	25·86	51·90
5·60	88·30	6·10	33·81	27·09	39·10
7·15	87·60	5·25	40·70	29·00	30·03
10·72	85·30	3·98	46·30	32·58	21·12
12·98	83·20	3·82	49·44	35·66	14·90

Table 2

Equilibrium Data for the System Ethylene Glycol — Ethyl Formate — Water at 30°C.

Solubility Data			Weight Percentage		
Glycol	Ethyl Formate	Water	Glycol	Ethyl Formate	Water
—	8·96	91·04	69·00	13·98	17·02
9·75	9·05	81·20	72·57	16·43	11·00
12·80	9·00	78·20	75·42	24·58	—
17·38	9·08	73·54	—	96·35	3·65
26·51	9·49	64·00	4·78	93·97	1·25
40·07	9·55	50·38	8·54	90·82	0·64
56·96	10·60	32·44	10·80	88·74	0·46
60·43	11·20	28·37	13·13	86·87	—

TIE LINE DATA

Ester Phase Composition Wt. %			Water Phase Composition Wt.%		
Glycol	Ethyl Formate	Water	Glycol	Ethyl Formate	Water
1·15	96·00	2·85	17·80	8·90	73·30
2·50	95·40	2·10	28·57	9·43	62·00
4·80	93·60	1·60	40·90	9·50	49·60
7·40	91·40	1·20	51·30	10·10	38·60
11·20	88·20	0·60	66·50	12·90	20·60

Table 3

Equilibrium Data for the System Ethylene Glycol — Cyclohexanon — Water at 30°C.

Solubility Data			Weight Percentage		
Glycol	Cyclohexanon	Water	Glycol	Cyclohexanon	Water
—	7·52	92·48	—	92·76	7·24
9·58	8·22	82·20	12·40	79·52	8·08
17·50	8·70	73·80	20·48	70·42	9·10
32·02	10·32	57·66	27·88	60·90	11·12
40·00	14·66	45·34	33·13	52·97	13·90
45·24	20·00	34·76	37·52	46·56	15·92
45·03	29·10	25·87	42·34	37·46	20·20

TIE LINE DATA

Cyclohexanon Phase Composition Wt. %			Water Phase Composition Wt. %		
Glycol	Cyclohexanon	Water	Glycol	Cyclohexanon	Water
1·30	91·00	7·70	14·60	8·65	76·75
3·45	88·70	7·85	26·75	9·75	63·50
5·24	86·80	7·96	34·90	11·50	53·60
8·04	83·80	8·16	41·70	15·60	42·70
11·80	79·90	8·30	46·00	22·20	31·80

Table 4

Equilibrium Data for the System Ethylene Glycol — Methyl Isobutylketone — Water at 30°C.

Solubility Data			Weight Percentage		
Glycol	Methyl Isobutylketone	Water	Glycol	Methyl Isobutylketone	Water
—	1·61	98·39	88·48	11·52	—
17·34	1·62	81·04	—	97·55	2·44
41·47	2·31	56·12	3·00	95·55	1·45
59·00	2·68	38·32	4·31	95·16	0·53
70·20	4·19	25·61	5·28	94·72	—
84·53	7·93	7·54	—	—	—

TIE LINE DATA

Ketone Phase Composition Wt. %			Water Phase Composition Wt. %		
Glycol	Methyl Isobutylketone	Water	Glycol	Methyl Isobutylketone	Water
0·49	97·20	2·01	18·41	1·39	80·20
1·40	96·50	2·10	35·12	2·08	62·80
2·30	96·00	1·70	56·84	2·36	40·80
3·90	95·40	0·70	69·73	3·77	26·50

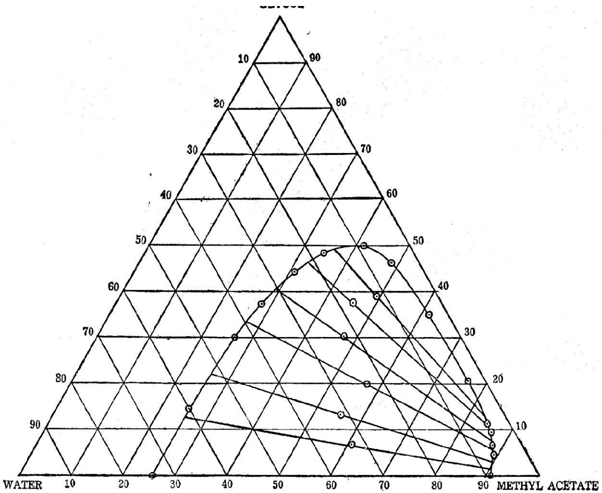

FIG. 1. Ethylene Glycol—Methyl Acetate—Water System

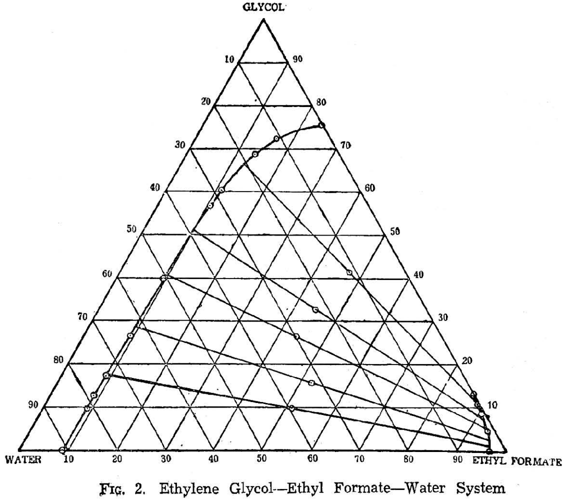

FIG. 2. Ethylene Glycol—Ethyl Formate—Water System

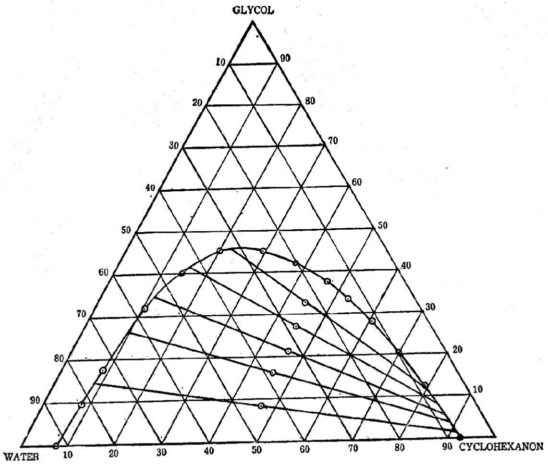

Fig. 3. Ethylene Glycol—Cyclohexanon—Water System

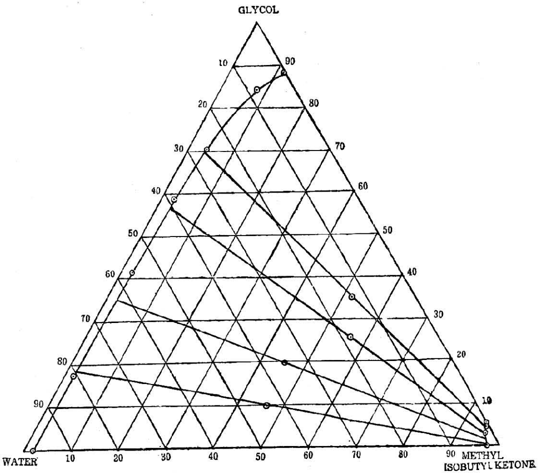

Fig. 4. Ethylene Glycol—Methyl Isobutyl Ketone—Water System

A simple curve for the distribution of glycol in the aqueous layer and solvent layer can be obtained by plotting weight percentage of glycol in aqueous phase against weight percentage of glycol in solvent phase. This has been done in Figure 5. The

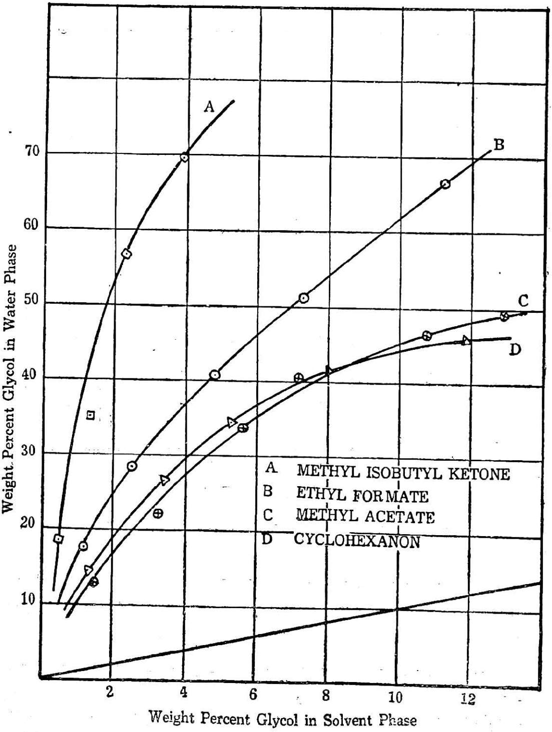

FIG. 5. Equilibrium Distribution Diagram

curves in Figure 5 give a comparison of the ability of the solvents to extract glycol from aqueous solutions.

Various methods have been suggested for smoothing and interpolation of phase distribution data. Figure 6 gives the Othmer and Tobias plot for the present data. The tie line data for all the systems have also been plotted as suggested by Bachman in Figure 7. It may be observed that both the correlations fit the

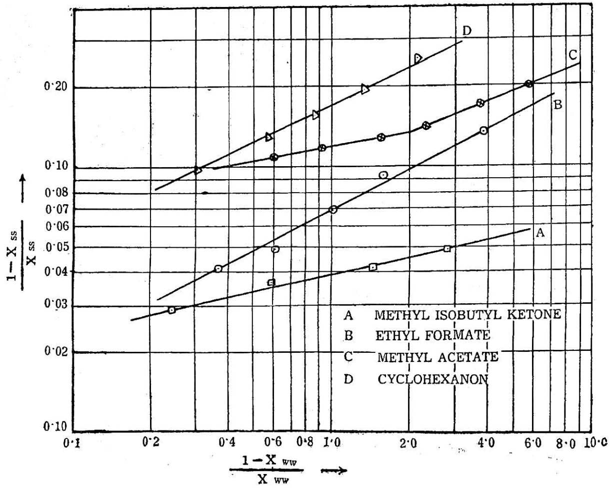

FIG. 6. Othmer and Tobias Plot of the Line Correlation

data well. The advantage of the correlations illustrated in Figure 6 and Figure 7 is that complete tie line information can be obtained with minimum experimental data.

It may be observed that ternary systems of glycol and water with ethyl formate and methyl isobutyl ketone comprise of one pair of miscible liquids and two pairs of partially miscible liquids and therefore are not expected to have plait points. However plait points have been determined for the systems glycol-water-methyl acetate, and glycol-water-cyclohexanon following the method suggested by Treybal, Weber and Daley (1946). This has

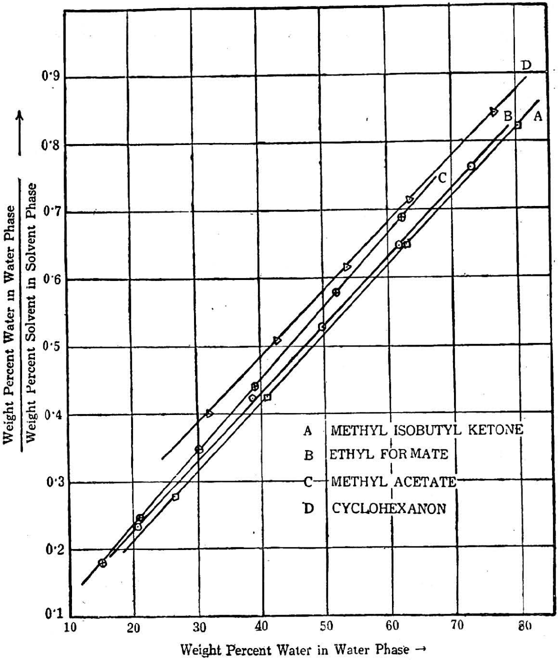

FIG. 7. Bachmans Plot of Tie Line Correlation

been shown in Figure 8 where on the plot of $\frac{X_{cs}}{X_{ss}}$ vs. $\frac{X_{cw}}{X_{ww}}$ giving the tieline correlation according to Hand (1930), the limiting solubility curve is also plotted as $\frac{X_c}{X_s}$ vs. $\frac{X_c}{X_w}$. As at the plait point the distinction between the water rich layer and solvent rich layer vanishes, the inter-section of the tie line correlation with the limiting solubility curve represents the plait point for the respective ternary system. The plait point for the system glycol-water-methyl acetate corresponds to 23·7% glycol, 73·1% methyl acetate and 3·2 % water. Similarly the plait point for

the system glycol-water-cyclohexanon represents the composition 21·8% glycol, 9·8% water and 68·4% cyclohexanon.

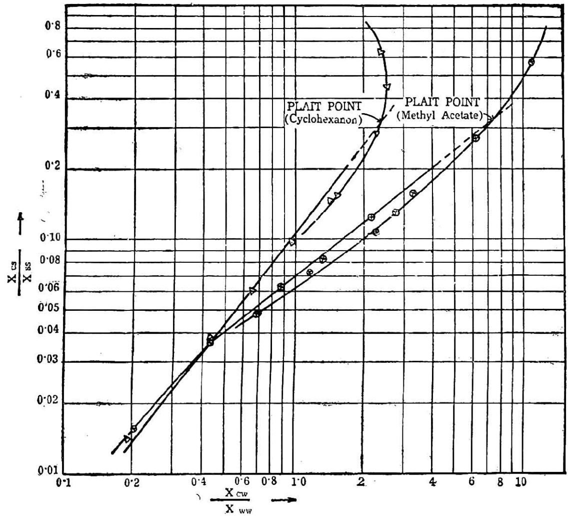

FIG. 8. Hands Plot of Tie Line Correlation

It may be observed that in the case of the ternary system glycol-water-methyl acetate, the solubility curve obtained shows a deviation from the normal pattern at the low glycol concentration for the solvent rich portion of the curve indicating that the solubility of water in methyl acetate decreases with addition of glycol. Such deviations from ideality have also been observed in other ternary systems such as phenol-water-aniline (1952) and acetone-water-phenol (1941).

Notation

X_{cs}	Weight fraction of glycol in solvent layer
X_{cw}	Weight fraction of glycol in water layer
X_{ss}	Weight fraction of solvent in solvent layer
X_{ww}	Weight fraction of water in water layer
X_c	Weight fraction of glycol
X_s	Weight fration of solvent
X_w	Weight fraction of water

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Commentaria Herbarii

Herbarium Collegii Presidentiae Madrasensis

6. Enumeration of plants collected in Mundanthurai and its neighbourhood (Tirunelveli District)

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ABSTRACT

349 species of flowering plants and 12 species of ferns collected from Mundanthurai and its neighbourhood (Tirunelveli District) have been recorded. Field notes for some of the plants have also been appended.

A perusal of Gamble's Flora of the Madras Presidency and the brief floristic analysis recently presented by Mudaliar and Sundararaj (1954) indicates that Tirunelveli District contains largest concentration of angiospermous taxa of the Madras Presidency (undivided). A detailed flora of the district, we learn, is under preparation, and in view of which endeavour a publication of an enumeration of plants occurring in a small locality of the Tirunelveli District is deemed to be useful not only as a supplementary source data for the compilation of the district flora, but also as a check-list for a specific locality, where a fairly intensive collection has been made during a particular season of the year. Although the scope of such a list is necessarily limited, we believe, that it represents a fair cross-section of plant taxa that bear flowers or fruits in one season of the year.

In spite of the long history of plant collection in Tirunelveli district, there are yet certain localities in it that need an intensive study, Mundanthurai and its environments belong to this category. The present list represents the plants collected during early February, 1958, the itinerary being as follows (Fig. 1):—

5—2—1958. Mundanthurai Forest Rest House and environs.

6—2—1958. Kodamadi, about 5 miles from Mundanthurai (Herbarium numbers 2196 — 2284).

7—2—1958. Karyar to about a mile short of Kannikatti Forest Rest House, a distance of about 6 miles (Herbarium numbers 2285 — 2355A).

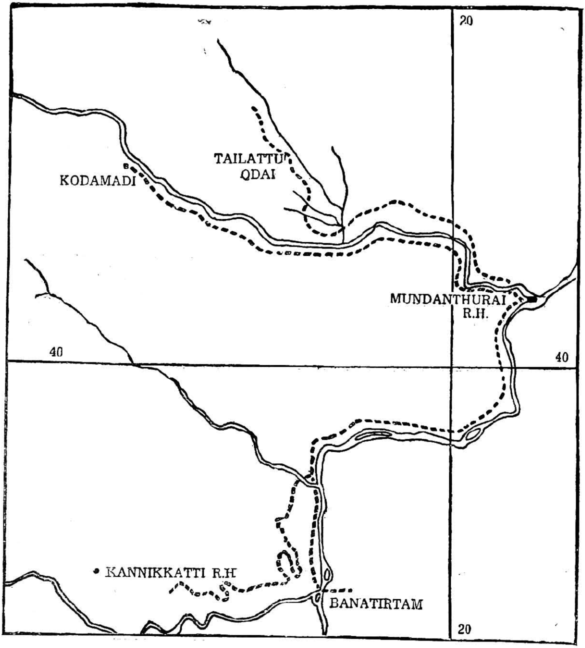

FIG. 1. Mundanthurai and environs, traced from Survey of India Topo-sheet n. 58 H/6, 1916, to show the routes of collection (broken lines). It may be noted, however, that the topography has now become slightly modified due to Papanasam Hydro-electric Project.

8—2—1958. Banatirtham and Kadavetti parai areas (Herbarium numbers 2356 — 2435).

9—2—1958. Koilteri and Tailattu Odai area, about 4 miles from Mundanthurai (Herbarium numbers 2436 — 2502).

As the localities covered during the excursion lie within a radius of five or six miles from Mundanthurai, the names of specific places are not cited in the list. As all the annotated specimens are deposited in the Herbarium Collegii Presidentiae Madrasensis, those interested in knowing either the specific localities or any other field information are welcome to consult the herbarium or through correspondence. Non-prefixed field numbers against plant names indicate the HCPM collections made by the authors and those that are prefixed by alphabets represent the collections of the student members of the party as given below: A — Alamelu, C — Chidambaram, I — Indra, K — Kamath, L — Lakshmi, N — Neelambal, R — Rajasekharan, S — Shanthi, Sr — Saraswathi, SS — Shanta Sarangapani, Sz — Shanaz, V — Viswanathan.

In addition, we have also included a few species which were seen but not collected. Such plants are indicated by an asterisk.

The vegetation of the area covered during the excursion varies from dense scrub to semi-moist evergreen types (Kannikatti and Kodamadi); sometimes opening out into grass lands here and there (Kadavetti parai). In the vicinity of Mundanthurai for a radius of four miles, the vegetation presents a rather uniform appearance in so far as the floristic composition is concerned, although the density of vegetation and the sylvicultural features of arborescent taxa appear to vary considerably as determined by rain fall. It is only beyond the four-mile radius that the vegetation begins to change, rather suddenly, into semi-evergreen belts. It is perhaps this situation that is implied in Ramaswami's (1914) statement that, "After leaving Mundanthurai (to Kannikatti) our march lay across forests." The majority of our collections were made within the four-mile radius.

Ramaswami's itinerary indicates that he must have had just a day or so (February 19, 1913) to explore Mundanthurai proper. Incidentally, we have also collected in this area in the same season of the year. He mentions nearly 90 species as occurring in this locality. There are only 36 species in the present list that have already been mentioned by Ramaswami as occurring in Mundanthurai, as against 313 of the present enumeration.

We are thankful to Dr. K. Subramanyam, Regional Botanist, Botanical Survey of India, Southern Circle, Coimbatore, for his help rendered in the determination of the Annonacean taxa.

ENUMERATION

Acanthaceae

Asystasia travancorica Bedd. 2331, 2372
Barleria cristata Linn. 2314
B. mysorensis Roth. R 219
B. prionitis Linn. 2449
Cardanthera balsamica Cl. R 237
Diotacanthus albiflorus Benth. 2229, 2255, 2318
Dipteracanthus prostratus (Poir.) Nees A 187
Ecbollium linnaeanum Kurz 2228
Justicia diffusa Willd. var. *hedyotifolia* C. B. Clarke 2411
J. glauca Rottl. 2325, A 142
Rostellularia serpellifolia (Gamble) Brem. 2216, 2421
Ruellia tuberosa Linn. N, no number
Rungia repens Nees 2326, N 214
Stenosiphonium parviflorum T. And. 2292, 2328
Thunbergia alata Bojer ex Sims. 2366

Amaranthaceae

Achyranthes aspera Linn. C. 143
Aerva lanata Juss. 2452, Sz 55
A. monsoniae Mart. Sz 55
Alternanthera echinata Sm. 2446
Amaranthus spinosus Linn. 2458
A. viridis Linn. 2244
Cyathula prostrata Bl. 2351
Gomphrena decumbens Jacq. Sz 97
Psilotrichum calceolatum Moq. 2198

Amaryllidaceae

Molineria finlaysoniana Baker 2355, 2489

Anacardiaceae

Nothopegia heyneana Gamble 2315

Ancistrocladaceae

Ancistrocladus heyneanus Wall. 2240

This plant does not appear to be as rare as generally presumed. The difficulty in identification in the field is perhaps due to the rather peculiar sylvicultural habit. It is interesting to note that, although the plant assumes a woody lianous habit when fairly well grown, younger plants are typically shrubby and relatively unbranched. The attainment of climbing habit is belated in ontogeny.

Annonaceae

Mitrephora heyneana Thw. 2245, L 66, K 92
Polyalthia korinti Benth. 2267, L 180
Unona pannosa Dalz. L 124

Apocynaceae

Aganosma cymosa G. Don *
Alstonia venenata R.Br. 2360
Carissa spinarum Linn. R 232
Ichnocarpus frutescens R.Br. R 35

Araceae

Pothos scandens Linn.*
Rhaphudophora pertusa Schott.

Aristolochiaceae

Aristolochia indica Linn. 2263, 2413, 2459
A. tagala Cham. 2352

Asclepiadaceae

Ceropegia elegans Wall. 2209
C. tuberosa Roxb. SS 77
Cryptolepis buchanani Roem. & Sch. R 70a
C. grandiflora Wt. R 74
Gymnema sylvestre R.Br. 2476
Hemidesmus indicus R.Br. 2231, 2294
Marsdenia volubilis T. Cooke A 14
Pergularia extensa N.E.Br. V 22
Secamone emetica R.Br. 2230, R 76

Balanophoraceae

Balanophora sp. 2355a

Begoniaceae

Begonia albo-coccinea Hook.*
B. crenata Dryand I 107
B. malabarica Lamk. 2347

Bixaceae

Hydnocarpus alpina Wt. 2277

Boraginaceae

Cordia monoica Roxb. 2448
Ehretia microphylla Lamk. 2473
Heliotropium bracteatum R.Br. 2327
H. scabrum Retz. L 96
Rotula aquatica Lour. 2237

Burseraceae

Commiphora caudata Engl. 2241, 2424

Caesalpiniaceae

Bauhinia sp.*
Cassia mimosoides Linn. R 210
C. timoriensis DC. 2442a
C. tora Linn. 2375

Capparidaceae

Cadaba trifoliata Wt. & Arn. 2401
Capparis sepiaria Linn.*
Cleome monophylla Linn. I 176

Caryophyllaceae

Polycarpaea corymbosa Lam. I 49

Commelinaceae

Aneilema montanum Wt. 2280
Commelina ensifolia R.Br.*
C. kurzii Clarke 2407
C. paleata Hassk. 2491
Cyanotis arachnoidea Clarke 2399
C. cristata Schult. f. 2224, 2398
Murdania semiteres (Dalz.) Santapau 2286, 2382

Compositae

Acanthospermum hispidum DC 2207
Ageratum conyzoides Linn. 2291
Bidens pilosa Linn. Sz 145
Blainvillea latifolia (Linn. f.) DC 2495
Blepharispermum petiolare DC 2205
Elephantopus scaber Linn. 2274, 2416
Emilia flammea Cass. 2389
Gynura lycopersicifolia DC 2406
Synedrella nodiflora Gaertn. C 215
Vernonia cinerea Less. L, no number
V. setigera Arn. 2320
Vicoa indica (Willd.) DC 2442, L 176

Convolvulaceae

Convolvulus ?flavus Willd. R 57
Evolvulus alsinoides Linn. 2381
Ipomaea ?angulata Lamk. 2412
I. obscura Ker.-Gawl. R 22
I. pes-tigridis Linn. 2477
I. rumicifolia Choisy L 153
I. staphylina Roem. & Sch. 2307
Merremia tridentata Hallier f. 2479

Crassulaceae

Bryophyllum pinnatum Kurz 2385

Cucurbitaceae

Bryonopsis laciniosa Naud. 2226
Coccinia indica Wt. & Arn. 2212
?Gymnopetalum wightii Arn. 2346, 2423
Melothria perpusilla Cogn. 2397

Cyperaceae

Fimbristylis annua Roem.. & Sch. var. *diphylla* Kuk. 2434
Kyllinga melanosperma Nees 2430
Lipocarpha argentea R.Br. 2429
Pycreus pumilis Dom, 2432
Scleria lithosperma Sw. var. *roxburghii* Thw. 2265

Dioscoreaceae

Dioscorea hispida Dennst. 2215
D. tomentosa Koenig. & Roxb. 2264
Trichopus zeylanicus Gaertn. 2348

This plant occurs more abundantly on road-side cuttings in sholas. We collected this plant enroute Kannikatti in semi-evergreen belt.

Eriocaulaceae

Eriocaulon collinum Hook. f. 2383
E. quinqueangulare Linn. 2379

Euphorbiaceae

Acalypha ciliata Forsk. 2196
A. paniculata Miq. R 194
Actephila excelsa Muell.-Arg. 2219, Sr 433
Aporosa bourdillonii Stapf 2317
A. lindleyana Baill. SS 109
Blachia calycina Benth. 2201.
B. denudata Benth. S, no number
Breynia rhamnoides Muell.-Arg. 2334
Bridelia roxburghiana Gehrm. 2243
B. tomentosa Bl. 2336
Coelodepas calycinum Bedd. C 156
Croton klotzchianus Thw. 2268, 2453
C. oblongifolius Roxb. SS 134
Dalechampia indica Wt. 2235
*Emblica officianalis Gaertn.**
Excoecaria crenulata Wt. 2246
Euphorbia fimbriata Heyne 2441
E. hirta Linn. 2394
E. pycnostegia Boiss. 2281
Gelonium lanceolatum Willd. 2206
Hemicyclia sepiaria Wt. & Arn. 2250, S 87
Jatropha glandulifera Roxb. 2436
Macaranga peltata Muell.-Arg.*
Mallotus distans Muell. Arg. C 196
M. philippinensis Muell.-Arg. 2248, 2247, 2340, 2297, 2456
M. repandus Muell.-Arg. 2435
M. rhamnifolius Muell.-Arg. 2341
Micrococca mercurialis Benth. 2469
Phyllanthus maderaspatensis Linn. Sz 77
P. niruri Linn. 2391
P. polyphyllus Willd. 2409
P. rheedii Wt. 2276
Sebastiania chamaelea Muell.-Arg. 2388

Gentianaceae

Canscora decurrens Dalz. S 110a
C. sessiliflora Roem. & Sch. 2302
C. wallichii C. B. Clarke 2223, 2422
Exacum sessile Linn. R 171

Geraniaceae

Biophytum insignis Gamble 2284

Kodamadi, where this plant has been collected, is the Type locality for this species.

B. longibracteatum Tad. & Jac. 2425

This species also appears to have been first collected in Mundanthurai. The authors of the species, however, do not mention the specific locality in their publication. We have collected this specimen from Banathirtham and Kadavetti parai. As far as we know, there are no record of this species outside Mundanthurai until now.

B. sensitivum DC. 2493, 2494

We take this opportunity to observe that the delineation of specific and subspecific categories of the genus *Biophytum* that occur in Madras Presidency is rather confusing. A preliminary survey of available collections of this genus has indicated that there is clear scope for a more detailed revision of the genus and for a more dependable artificial key for the identification of the species. A taxonomic revision as pertaining to the species in Madras Presidency is under progress in this Herbarium.

Oxalis corniculata Linn. 2270, C 165

Gesneriaceae

Didymocarpus humboldtiana Gardn. 2419.

Gramineae

Alloteropsis cimicina Stapf R 28
Chrysopogon hackelii C.E.C. Fisch. 2427
Cymbapogon confertiflorus Stapf 2428
C. caesius Stapf A 117
Eragrostis pilosa Beauv. R 205
E. tremula Hochst. 2288
E. willdenoviana Nees R 197

Iseilema laxum Hack. 2287
Perotis indica O. Ktz. A 10
Rhynchochelytrum villosum Chiov. R 203
Sporobolus diander Beauv. Sr 409
Themeda cymbiaria Hack. 2426
Urochloa panicoides Beauv. Sz. 130

Ficoideae

Mollugo pentaphylla Linn. 2300, 2378, 2485

Hippocrateaceae

Loeseneriella obtusifolia (Roxb.) A.C.Sm. R 150

Labiatae

Anisochilus paniculatus Benth. 2305
A. wightii Hook. f. 2306
Anisomeles malabarica R.Br. 2444
Geniosporum prostratum Benth. 2338, L 106
Hyptis suaveolens Poit. A 15
Leonotis nepetaefolia R.Br. 2482
Leucus biflora R.Br. 2322, 2492
L. ?cephalotus Spreng. 2475
L. ?nutans Spreng. 2376
Ocimum americanum Linn. 2362, 2377
O. gratissimum Linn. 2213
O. sanctum Linn. 2254, 2438, 2466
Orthosiphon glabratus Benth. A 77
O. pallidus Roxb. L 106a
Scutellaria violacea Heyne 2232, N 65

Lauraceae

?Cinnamomum sp. 2345

Lentibulariaceae

Utricularia sp. 2384
U. caerulea Linn. 2357
U. striatula Sm. 2364

Liliaceae

Chlorophytum heynii Baker 2311
C. laxum A.Br. 2266
Dianella ensifolia Red. 2312
Dracaena terniflora Roxb. 2343
Smilax zeylanica Linn. 2332, L 145

Linaceae

Erythroxylon monogynum Roxb. 2450
Hugonia mystax Linn. 2463

Loganiaceae

Fagraea obovata Wall.*
Strychnos bicirrhosa Lesch. C 135

Loranthaceae

Loranthus buddleioides Desv. 2470
L. longiflorus Desv. 2298
Viscum heyneanum A.P. de Cand. 2415
V. orientale Willd. 2269

Lythraceae

Ammannia baccifera Linn. var. *aegyptiaca* Koehne 2461
Nesaea lanceolata Koehne 2414

Malpighiaceae

Hiptage madablota Gaertn.*
H. parvifolia Wt. & Arn. R 229

Malvaceae

Hibiscus platanifolius Sweet 2285
H. solandra L'Her. 2272
H. surattensis Linn. 2330, 2396
H. vitifolius Linn. SS 164
Pavonia odorata Willd. I 72
P. zeylanica Cav. 2211
Salmalia malabarica Sch. & Endl.*
Sida acuta Burm. 2273
S. cordifolia Linn. 2261, 2496
S. rhombifolia Linn. var. *retusa* Mast. 2488
S. rhomboidea Roxb. 2400
S. veronicaefolia Lam. 2350, 2405

Melastomaceae

Osbeckia aspera Bl. R. 179, 2363
O. octandra DC. C 282
O. zeylanica Willd. 2258, 2295

Meliaceae

Aglaia roxburghiana Hiern. 2440
Cipadessa baceifera Miq. 2323
Walsura piscidia Roxb. L 116

Menispermaceae

Cocculus hirsutus Diels Sr 340

Mimosaceae

Albizzia lebbeck Benth. L 179
A. marginata Merr. L 107
Dichrostachys cinerea Wt. & Arn. 2437
Mimosa pudica Linn. 2417, Sr. 260
Pithecellobium dulce Benth. SS 171

Myrsinaceae

Embellia basaal A.DC. 2439
Maesa perrottetiana A.DC.*

Myrtaceae

Eugenia jossinia Duthie R 145
E. singampattiana Bedd. 2296
Syzygium arnottianum Walp. 2358

Opiliaceae

Cansjera rheedii Gmel. 2214

Oleaceae

Jasminum calophyllum Wall. 2221, 2278
Linociera courtallensis Bourd. 2395
L. zeylanica Gamble 2238

Onagraceae

Ludwigia parviflora Roxb. 2251.
L. prostrata Roxb. 2257

Palmaceae

Calamus travancoricus Bedd. 2304

Papilionaceae

Alysicarpus hamosus Edgew. 2374
A. rugosus DC. var. *styracifolius* Baker 2369, 2408

Clitoria ternatea Linn. 2447
Crotalaria albida Heyne 2337
C. clavata Wt. & Arn. 2309
C. verrucosa Linn. 2329, 2486
Derris scandens Benth. N 196
Desmodium gangeticum DC. SS 182
D. latifolium DC. C 154
D. triflorum DC. 2471
Indigofera hirsuta Linn. 2279
I. parviflora Heyne R 7, 2481
I. pulchella Roxb. 2335, Sr 432
Mucuna monosperma DC. 2484
Phaseolus dalzellii T. Cooke 2403
P. mungo Linn. 2260 (cult.)
P. sublobatus Roxb. L 5
Pseudarthria viscida Wt. & Arn. 2262, 2402
Rhynchosia viscosa DC. 2239, 2308
Stylosanthes mucronata Willd. 2472
Tephrosia hirta Ham. 2467
Teramnus labialis Spreng. 2253
Zornia diphylla Pers. 2321, 2420
Z. zeylonensis Pers. C 107

Passifloraceae

Adenia palmata Lamk. 2501, 2502

This species is a large climber, branching after reaching a height of 20 ft. or more on the supporting-tree. The roots have been described as being tuberous. In 2501, we found that the basal part of the stem (about 2 feet from the ground) was swollen to a diameter of nearly 1 ft., somewhat abruptly tapering towards the apex. The swollen part exhibits a remarkable method of increase in girth of the stem. The results of this study will be published elsewhere.

Passiflora calcarata Mast. 2220

Piperaceae

Piper galeatum Cas. DC. 2289

Polygalaceae

Polygala javana DC. 2225, 2380

Polygonaceae

Polygonum chinense Linn. L, no number

Plumbaginaceae

Plumbago zeylanica Linn. 2457

Nyctaginaceae

Pisonia aculeata Linn. 2203, 2242, 2490

Rhamnaceae

Ventilago bombaiensis Dalz. C 117
V. maderaspatana Gaertn. 2204, 2460

The plants were only in flowers. In view of the keys for identification being based on the characters of the fruit, and in view of rather limited specimens available for comparison, the determinations given above are provisional.

Zizyphus mauritiana Lamk. 2487
Z. mauritiana Lamk. var. *fruticosa* Haines I 158
Z. oenoplia Mill. 2483

Rubiaceae

Borreria hispida K. Sch. 2410
Gardenia gummifera Linn. f. R 85
Ixora nigricans Br. 2316
Mitragyna parvifolia Korth. 2465
Mussaenda frondosa Linn. 2293
M. ?laxa Hutch. I 159
Oldenlandia albo-nervia Gamble 2259, 2324, 2404, 2468
O. herbacea Roxb. 2342, 2368
O. purpurascens O. Kze. var. *pallida* Gamble 2359
O. umbellata Linn. 2333
Ophiorrhiza mungos Linn. 2271
Pavetta breviflora DC. 2339
P. indica Linn. 2200
Plectronia didyma Kurz 2202
Psychotria bisulcata Wt. & Arn. 2356
P. macrocarpa Hook. f. 2349, 2418
Randia dumetorum Lamk. 2365
R. malabarica Lamk. 2210, 2233

Tarennia asiatica (Linn.) O. Ktze. (*Chomelia asiatica O. Kze.*) SS 67
Wendlandia notoniana Wall. 2254

Rutaceae

Atalantia racemosa Wt. & Arn. 2208, 2455
Clausena willdenovii Wt. & Arn.*
Glycosmis pentaphylla Correa R 217
Murraya exotica Linn. R 157
Toddalia asiatica Lamk. var. *gracilis* Gamble 2500
T. asiatica Lamk. var. *obtusifolia* Gamble N 185

Samydaceae

Homalium travancoricum Bedd. K 80
H. zeylanicum Benth. 2344

Santalaceae

Santalum album Linn. 2451
Scleropyrum wallichianum Arn. 2236

Sapindaceae

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Filicium decipiens Thw. I 153
Sapindus emarginatus Vahl. I 63

Sapotaceae

Isonandra lanceolata Wt. 2313

Scrophulariaceae

Ilysanthes veronicaefolia Urb. N 168
Lindernia ciliata (Colsman) Pennell 2299, 2373
Scoparia dulcis Linn. 2370
Sopubia delphinifolia G. Don 2480
S. trifida Ham. 2361
Vandellia crustacea Benth. 2301, 2478

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Physalis minima Linn. SS 71
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S. verbascifolium Linn. 2227, A 200

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Melochia corchorifolia Linn. S 2
M. nodiflora Sw. I 178

This is apparently an introduced plant.

Waltheria indica Linn. 2222, Sz 75

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Corchorus acutangulus Lamk. 2252.
C. aestuans Linn. 2386
C. tridens Linn. N 31
Grewia flavescens Juss. 2443
G. heterotricha Mast. I 66
G. hirsuta Vahl. 2310.
G. orientalis Linn. 2199, 2282, 2445
Triumfetta annua Linn. 2390
T. pentandra A. Rich. Sz. 56
T. rhomboidea Jacq. 2275

Urticaceae

Celtis wightii Planch. 2499
*Plecospermum spinosum Tréc.**
Pouzolzia bennettiana Wt. var. *macrophylla* Hook. f. 2353, 2393
P. indica Gaud. 2387
P. ?wightii Benn. 2354, 2392
Streblus asper Lour. 2474
Trema orientalis Bl. 2303

Verbenaceae

Gmelina asiatica Linn. 2462
Lantana camara Linn. var *aculeata* Moldenke I 74
L. indica Roxb. L 144
Stachytarpheta indica Vahl. C 180
Tectona grandis Linn. f. 2498

Violaceae

Ionidium suffruticosum Ging, 2256
I travancoricum Bedd. C 160

Vitaceae

Ampelocissus tomentosa Planch. I 32
Cissus sp. L 172
Leea sambucina Willd. R 124

Ferns

Actiniopteris australis (L.f.) Link.
Adiantum caudatum L.
Asplenium contiguum Klfs.
A. praemorsum Sw.
Cheilanthus mysorense Wall.
Drymoglossum heterophyllum (L.) C. Chr.
Dryopteris sparsa (Ham.) O. Ktze.
Hemionites arifolia (Burm.) Moore
Microlepia speluncae (L.) Moore
Pteris quadriaurita Retz.
Pyrrosia adnascens (Forst.) Ching
Tectaria polymorpha (Wall.) Copel.

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